ZOOPLANKTON SPATIAL AND SEASONAL DISTRIBUTION IN BROOKLANDS LAGOON.

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By

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Contents

Errata:

Page 75, last sentence should read:
Deeper light penetration allows greater primary production and hence herbivorous zooplankton are found to greater depths in the daytime, over a wider range of phytoplankton concentrations.

Page 76, last paragraph sentence beginning, Bosch and Taylor (1973) should read:
Bosch and Taylor (1973) showed the cladoceran *Podon polyphemoides* had a reversed migration pattern with a diel photoperiodicity that kept it within the confines of Chesapeake Bay.

Figures and Tables

ABSTRACT

THE ECOLOGY OF ZOOPLANKTON OF BROOKLANDS LAGOON

The temporal and spatial distribution of zooplankton within Brooklands Lagoon was recorded at 3 sites representing a range of salinities and hydrographic conditions. Plankton tows were made monthly for one year to estimate seasonal abundance and distribution of zooplankton species. Diel distribution patterns were investigated in February by sampling at 3-hour intervals for a 30-hour period.

The 48 taxa identified within Brooklands Lagoon represent a depauperate fauna compared with the nearby Avon-Heathcote estuary and the Kaikoura coastal waters. Brooklands Lagoon had approximately one tenth of the zooplankton biomass found in the Avon-Heathcote estuary. Results of ordination analysis showed a succession of dominant groups: *Acartia* sp., *Microcyclops* sp., *Camptocercus* sp. and *Miscegenus heretunga* in the summer, followed by barnacle and copepod nauplii during the winter. Changes in zooplankton abundance and biomass were influenced more by river flow and the degree of seawater mixing, than season, chlorophyll a concentration or temperature.

Daily zooplankton abundance patterns were strongly influenced by darkness, resulting from the combined effect of turbidity and diel period. Zooplankton were also abundant during the early morning while chlorophyll a concentrations were increasing. The meroplankton showed high biomass and abundances during daytime high tides.

Gut analysis of larval mullet, *Mugil cephalus* showed a diet of cyclopoid copepods, ostracods and oligochaetes. The flatfish larvae, *Rhombosolea plebia*, revealed a high dependance on zooplankton, eating almost exclusively *Miscegenus heretunga*. This harpacticoid copepod had a temperature/ salinity tolerance between 1.7->40ppt. salinity

and <5-26°C over 24hours. This tolerance range is wider than the temperature and salinity ranges recorded in the lagoon.

INTRODUCTION

A paucity of basic research on estuarine zooplankton is evident in the New Zealand literature, despite the emphasis on their importance from overseas research. Although zooplankton forms the basis of many marine and estuarine foodwebs (Deevey 1960a, Voronia 1970) little is known of the inshore zooplankton around New Zealand. To date there has been a single estuarine survey of zooplankton in the South Island by Roper et. al (1983) who studied zooplankton in the Avon-Heathcote rivers estuary. Because this study was only carried out over a period of six months it was unable to investigate seasonal fluctuations of abundance but did manage to demonstrate spatial variances within the length of the estuary. This was the first list of zooplankton species present in the estuarine environment.

OCEANOGRAPHY

The water masses of the globe have been divided depending on physico-chemical parameters. A single water mass generally has a narrow definable range of oxygen concentration, temperature and salinity, which are normally stable. Transition zones and boundaries exist between the water masses (Van der Spoel and Hayman 1983). New Zealand is situated in between the 35th and 46th latitude south of the equator. This places it in a transition zone between the northern sub-antarctic water mass and the southern temperate waters. Around the southern part of the globe exists a band of waters connecting all the major oceans and placing New Zealand in the middle of an otherwise uninterrupted global current system. This current flow has been established by the continuous westerly winds and orbital spin.

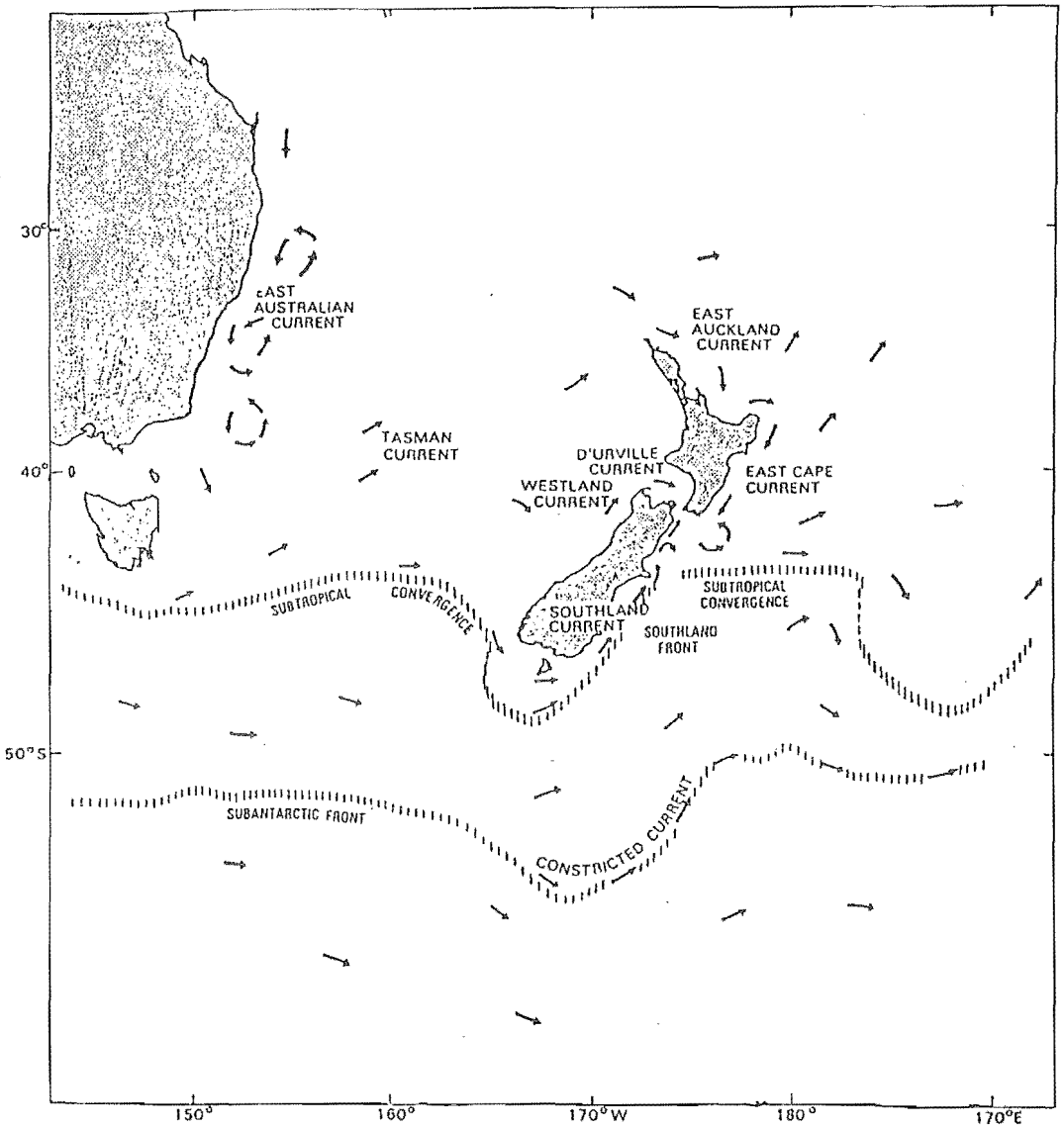


Fig. 1 Ocean currents and circulation around New Zealand.

New Zealand separates the colder subtropical westerly drift and warmer tropical Tasman currents. This zone of converging currents is the subtropical convergence zone and can be found around the south of the South Island, extending east from Kaikoura into the Pacific Ocean (Heath 1985) (Fig. 1). These water masses are theoretically divided by the Dunbar line (5°C surface isotherm). Depending on annual weather conditions and current regimes the Dunbar line may intersect the east coast of New Zealand between Hawke Bay and Banks Peninsula.

Each mass of water in this system retains some of the characteristics from its origins. These factors include lower temperatures and higher salinities of the colder waters and higher temperatures and lower salinities of the warmer waters. Faunal elements are also retained in this flow if they are unable to swim strongly enough to escape from it. Thus species of zooplankton can be used as indicators of the global origins of water masses. Species from warm temperate waters and colder regions can all be found mixed within the subtropical convergence zones around New Zealand (Grieve 1966). Neritic species usually occur in shallow water along coastlines. Distribution is determined by physico-chemical properties of the water, which are in turn usually above the 200m depth line (Raymont 1983).

ESTUARIES

Zooplankton in estuaries are poorly represented because they are limited by currents such as tidal flow, river flow, and salt wedge mixing. Zooplankton is also limited by turbidity (Mclusky 1981), but this is in direct contrast to findings in a local study by Roper et. al. (1983). In estuaries there is usually a limited zooplankton fauna represented by a few resident species such as *Acartia jilletti* and *Euterpina acutifrons* (Bradford pers. comm., Raymont 1983). Extreme

ranges in salinity and temperature due to shallowness and proximity to land make estuaries a severe environment in which to exist (Riley 1967). The permanent zooplankters found in this environment have two main mechanisms for survival. They may be able to tolerate wide fluctuations, being euryhaline and eurythermal and living in ranges of 2ppt to 40ppt and 0°C-25°C (Mclusky 1981). Laboratory experiments confirm these observations (Davis 1984, Conover 1964).

Alternatively in such an environment they may show behavioural adaptations allowing them to evade or seek shelter from fluctuating conditions. This latter strategy has been adopted by the meiofauna, which are often quite dense (Coull 1979, Coull & Wells 1981; Hicks and Coull 1983). These taxa, represented mainly by harpacticoid copepods, isopods and amphipods, become planktonic for the flood tide to feed and reproduce, while the remaining time is spent sheltering in the benthos. It is thought that meiobenthic species are often able to feed at the expense of the resident zooplankton (Riley 1967) especially where water is shallower than the euphotic zone. Estuaries are efficient detritus traps due to flocculation and hydrological processes (Barnes 1974) which eliminate much of the organic detritus from the water column inhabited by the zooplankton (Riley 1967).

Few authors estimate zooplankton biomass, but Mclusky (1981) states that it is much smaller than benthic population estimates. Estuaries are known to be able to support large zooplankton populations due to several reasons. Plant material breakdown is high from species such as *Spartina* sp.and *Juncus* sp. There is a large degree of microbial action in the water column, often caused by human discharge into this environment and often recorded high phytoplankton production (Mclusky 1981, Knox and Kilner 1973, Knox 1987).

STUDY AREA

Brooklands Lagoon is a shallow, coastal, river estuary situated 15 km north-east of Christchurch at the mouth of the Waimakariri River. The Brooklands Lagoon river estuary was formed in 1933 when, after flooding the nearby marshland country, the narrow coastal spit between the Waimakariri river and the sea was bulldozed through at Kairaki. This allowed a more direct emptying of flood waters from the Waimakariri river. The remaining river mouth closed forming the Brooklands Lagoon estuary (Figure 2). Although called a lagoon, Brooklands is strictly an estuary according to the definition of Cameron and Pritchard (1963), "an estuary is a body of shallow water with a free connection to the sea, where seawater is measurably diluted by freshwater from terrestial runoff". Brooklands Lagoon estuarine system has had few previous studies made on it. A report by Knox and Bolton (1977) sampled macro-invertebrate fauna and some physical and chemical variables. Their report suggested that the Brooklands estuary is an important nursery area for larval flatfish, which are planktivorous (Roper 1979, Mundy 1963).

The depth of the lagoon varies with the tidal cycle and shallows out further from the Waimakariri River. Depth ranges from zero when completely empty to one metre in primary channels at low tide. At high tide, depending on the lunar cycle, the deeper northern end may vary in depth from four to two metres deep. The Lagoon is subjected to an average twice daily tidal regime, which may be modified from the coastal cycle by retention times due to the bathymetry of the

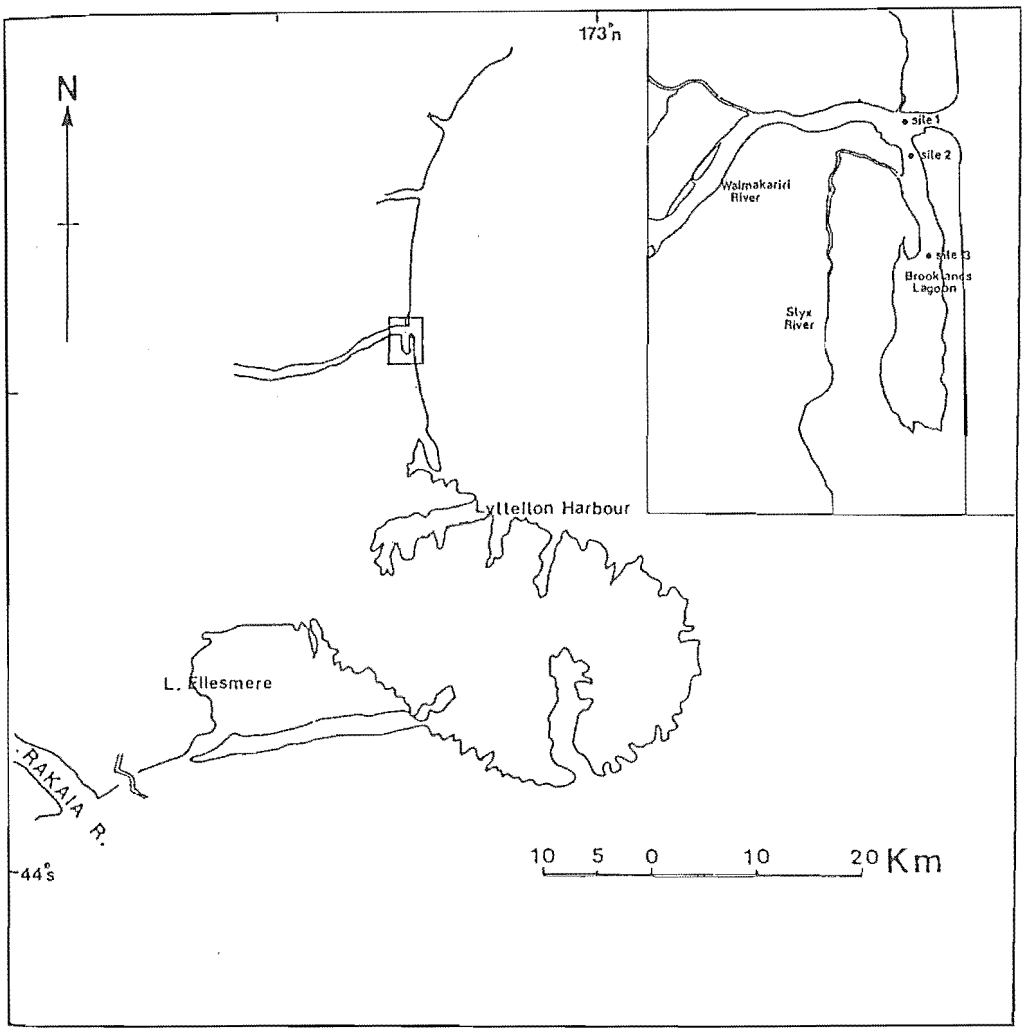


Fig. 2 Location of Brooklands Lagoon showing sampling sites.

lagoon bar. The lagoon covers an area of 170 ha. and has a spring tide volume of approximately 1.6x106m3 which is 90% flushed (Knox & Bolton 1977).

The freshwater inputs to this estuary are very large. These are mainly from the Waimakariri River, where the large volume of this river has reduced the salt water wedge entering the estuary to a narrow band. Initial sea-water dilution in the lagoon is by the Waimakariri River, which is continuous. There is a further dilution throughout the length of the lagoon by the Styx River (Knox & Bolton 1977). Sea water dilution is demonstrated through the Lagoon by the salinity range (0.5ppt to 3ppt) making it oligohaline by definition (Remane & Schliper 1971).

For this study three sampling sites were selected corresponding to those previously used by Knox and Bolton (1977) to study the macro-invertebrates of the lagoon (Fig. 2). These sites were also selected to represent the range of hydrographic and physico-chemical conditions within the lagoon. Site one was situated in the Waimakariri river 0.70 km from the sea and was the deepest station in the study area. This part of the Waimakariri River has a constant flow of river water which is increased by the incoming tide and river floods. The Styx River also flows out through this section of the Waimakariri River. All tidal flows must pass through this narrow area to fill and empty Brooklands lagoon.

Site two is situated within the lagoon proper 1.10 km from the sea. The Styx river maintains a constant minimum level at this site. The major portion of the water level at this site is from the incoming tide which floods the area to a depth ranging from two to four meters. This area and site three to the south are both currently being filled slowly by silt deposited when the Waimakriri River floods (Knox & Bolton 1977).

Site three is also within the lagoon proper, 2.30 km from the sea. This portion of Brooklands lagoon was formed when the Waimakariri river was re-channelled. At the present time this area of the lagoon has no freshwater flow through it. However flood tides mix with river waters to be diluted from coastal salinities in this upper area of the lagoon. This area of the lagoon is filling faster than the lower site two, as it does not have the clearing action of any freshwater flow through.

A monthly sampling regime was established to investigate patterns of zooplankton distribution and abundance within Brooklands lagoon. Analysis of the data will yield seasonal patterns of distribution and abundance. Separation of the data from the three sites will establish environmental and spatial patterns of zooplankton distribution. Further, species dominance indicies and changes in dominance correlated with fish gut analysis will show the basis of an estuarine food web.

CHAPTER ONE

ZOOPLANKTON FAUNA OF BROOKLANDS LAGOON

INTRODUCTION

Estuaries have wide ranging conditions of physical and chemical conditions which make a stressful environment for many species, especially those adapted to the marine environment, such as the copepods *Centropages aucklandicus* and *Temora turbinata*. Estuaries are often regarded as physically controlled environments (McLusky 1981) and species diversity is low. The most common species are those organisms which are more tolerant to temperature and salinity fluctuations. This includes the larval or dispersal stages of many vertebrates and invertebrates found in the meroplankton. The meroplankton often include the majority of animal groups present in the plankton in an estuary (Riley 1967), although their appearance may be brief and seasonal.

The temporary nature of the estuarine environment, due to silt loads deposited during river floods and coastal erosion, add further to the stress of this environment. This factor may also restrict the diversity of species within an estuary, because resident populations do not have time to mature in an evolutionary process (McLusky 1981).

Tolerance for the physical environment may be increased within a group of animals by adaptation, compensation or finally by speciation (Riley 1967). In this instance the newer species may be more tolerant at one extreme of tolerance of a particular physical variable, such as salinity or temperature, extending its tolerance to a wider range. Many studies have shown gradual replacement of species within a genus along the physiological gradients within an estuary. For example Jeffries (1962b) shows succession of two copepod species of *Acartia* along the salinity gradient of estuaries on the

East Atlantic sea coast. Mackas and Anderson (1986) show similar successions in the occurrence of euphausids along the temperature gradient within British Columbian fjords. Reduced salinity within estuaries often stresses neritic species. Those species normally resident in estuaries can maintain their position by behavioural adaptations and physical adaption. Barnes (1974) has noted that the estuarine *Acartia* species feeds inefficiently. This is probably due to the decreased diversity of species within an estuary reducing interspecific competition for food resources, which in turn would allow the existence of an inefficiently feeding species such as *Acartia*. Coastal species such as *Euterpina* feed much more efficiently due to the higher interspecific and intraspecific competition that they face. Many estuarine species would be unable to survive in coastal waters because of their poor grazing efficiency. Many coastal species are unable to survive in estuaries for long periods because of their more limited tolerance range for physical and chemical factors. Position of individuals within the preferred tolerance ranges is maintained by selective swimming behaviours. This mechanism keeps the animal in the tidal flow entering the required estuarine zone. Sandifer (1975) has shown that zoeae larvae of *Cancer* species and other decapods in Chesapeake Bay use vertical swimming behaviour to maintain position in optimal conditions within tidal flows.

Within an estuary, there are often some species which are permanent euryhaline residents. However there may also be large inputs of marine and freshwater species, due to the dynamic nature of the estuarine ecosystem. The species stationed permanently within the zooplankton (holoplankton) of the estuarine ecosystem can be divided into two major components. 1) Those that maintain their station within the estuary and are represented in the estuarine fauna

all year round. 2) The other component consists of the marine fauna and river drift species. Although stenohaline, the open coastal or offshore marine fauna are present within the estuary for a short part of each day and thus have time to recover from the stress of entering a lower salinity region. This group represents a large potential biomass input to the estuarine environment. However, due to the tidal currents a lot of biomass may be removed from an estuary by the ebb tide. Diversity of species within an estuary tends to decrease with a decreasing degree of tidal flushing. As the flushed component increases the diversity of the estuarine plankton may increase due to a greater input and diversity of forms from the open coastal environment (McLusky 1981).

Preference for and tolerance of environmental conditions differs between each zooplankton species and each stage in its life history. Species are often classified by eury- or steno- tolerance of factors such as temperature or salinity.

The occurrence of species and their distribution patterns, and abundances are influenced by environmental parameters which can be measured. Other influences especially the biological interactions such as predation pressure or competition for food may be unsuspected. Species distribution may also reflect distribution in climatic, geographical and biological dimensions. These factors may change in importance with time. Factors which may be currently important to the distribution of an organism may reflect conditions previously experienced. Species are often characterized by their common regional distribution range, that is neritic, temperate, sub-tropical, equatorial, benthic or bathy-pelagic.

Brooklands Lagoon estuary is less than one third of the area of the nearby Avon-Heathcote rivers estuary. In the inter-tidal range there are fewer representatives of several classes of

macro-invertebrates, notably, molluscs and decapods. The lack of macro-invertebrates may reflect a correspondingly depauperate plankton fauna, which forms the basis of the estuarine food-web. Another cause may be severe physiological stress due to pollution in Brooklands (Knox and Bolton 1977). Alternatively a depauperate fauna may be a reflection of the temporary and constantly changing environment of this estuary due to Waimakariri River flooding.

The aim of this section of my study was to record the zooplankton species present in Brooklands Lagoon. Comparisons will be made with similar habitats in other locations. Species present and their spatial distribution will establish the ecological status of Brooklands Lagoon. Differences that can be readily examined include, diversity of species and life history patterns of the major phyla.

METHODS

FIELD SAMPLING

Zooplankton trawls were made at three pre-selected sites within Brooklands lagoon (Fig. 2). Site one was situated at the mouth of the lagoon in the Waimakariri River, 0.75km from the sea. Site two was situated between the mouth of the Styx River and the mouth of Brooklands Lagoon 1.10 km from the sea and a third site was selected three-quarters of the way down the lagoon, 2.30km from the sea.

Sampling was carried out monthly from December 1985 through to December 1986. Each sample was taken on the incoming tide just prior to high tide, against the incoming tidal flow. The sampling day chosen for each month was a day that had high tides close to mid day. This method was chosen to make sampling conditions as uniform as possible in an attempt to reduce the sample variances .

During the summer, a diurnal survey was made at site two. In general the same methods were used for the diurnal survey as in the seasonal survey. Samples were taken every three hours during periods of high, low and mid tide for 39 hours. During each sampling period five replicate trawls were made and later subsampled three times to determine the taxa present. During this survey two complete tidal cycles were sampled and a single period of darkness.

Zooplankton trawls were made using a standard plankton net. 0.33m diameter, 0.33ìm mesh size. The net was towed at three k.p.h. for three minutes at each station every month. Five repeated tows were made at each site. This method has been shown by Cassie (1959), to reduce the standard error of calculated means. Bary (1959) has also shown by statistical analysis that frequent short tows and corresponding hydrographic measures provide a better index to overall surface conditions, especially where steep gradients may exist. For example in mixing waters such as estuaries and ocean current fronts.

LABORATORY ANALYSIS

In the laboratory each of the replicate trawl samples was sub-sampled three times to estimate species diversity and concentration. Sub-sampling was made using a 0.79 cm bore 10ml pipette after the sample was thoroughly shaken. After all the sub-samples were removed the remainder of the sample was passed through a coarse sieve to count larger animals that would not pass the pipette tip. The macro-zooplankton in each sub-sample were counted under an inverted microscope. This microscope had low power objectives for quickly counting and identifying most taxa, and high power lenses for accurate identification of smaller and more difficult taxa. During enumeration of the plankton samples identification was made to species level where possible.

Keys used for zooplankton identification were: Bradford (1972, 1976, 1978) for common calanoid copepods, separation of *Acartia* sub-species, *Temora turbinata* and *Paracalanus indicus* respectively. Wear (1985) and Wear & Fielder (1985) were used to identify the brachyuran zoeae and natant decapods. Wells, Hicks and Coull (1982) allowed accurate identification of the harpacticoid copepods. More recently described harpacticoid taxa were identified using Hicks (1971). These species included *Miscegenus heretunga* males and females, *Quinquelaophonte* sp. and *Halectinosoma* sp.

However time restraints limited identification to broad taxanomic levels in some cases. Although some errors may exist in the accuracy of some of my species identifications, I have attempted to keep these constant throughout each section of the study so that statistical analysis will not be disrupted. A general identification of taxa does not impair statistical analysis as higher taxa in these cases were often represented by single occurrences of one species.

RESULTS

SPECIES LIST

The species list of zooplankton found within Brooklands Lagoon is included in Table 1, which includes 48 separate taxa, divided into groups of meroplankton (18 separate taxa) and holoplankton (30 separate taxa).

The total list of 48 taxa contains some rare taxa represented by a single occurrence of an unidentified (to species level) specimen. For example the actinotroch larvae of the phoronid worm which was most likely *Actinotrocha branchiata*. The appearance of the free swimming individual larvae of a cryptoniscid isopod was observed during several months at a single site only. This stage is generally very brief because the larva hatches from the intermediate crab host and quickly moves through the water to its final position as an external parasite of an unknown fish species host. Similarly adult amphipods and isopods occurred infrequently and were not identified beyond their respective orders as their numbers were so low.

Acartia jilletti and *A. clausii* were both very common throughout the study sites, but during counting they were grouped as a single genus. Aggregation of *Acartia* sp. to a single genus was made during counting to shorten processing times.

TABLE ONE List of Taxa from Brooklands Lagoon.

Meroplankton

Barnacle nauplii — *Elminius modestus*
cyprids
Copepod nauplii
Brachyuran zoea — *Macrophthalamus hirtipes*
megalopae
Anomuran zoea — *Petrolisthes elongatus*
Euphausid nauplii
calyptopis
Polychaetes trochophore
enteropneust tornaria
phoronid actinotroch *Actinotrocha branchiata*
Isopoda, Crytoniscidae (new species)
Gastropod veligers
Bivalve veligers
Echinoderm pluteus
biplanaria
Teleost eggs
larvae: unknown
Galaxiidae

Holoplankton

Crustacea:
Copepoda:

Calanoida:	Harpacticoida:	Cyclopoida:
Acartia jilletti	*Miscegenus heretunga*	*Oithona similis*
Acartia clausii	*Euterpina acutifrons*	*Microcyclops* sp.
Paracalanus indicus	*Quinquelaophonte* sp.	
Temora turbinata	*Halectinosoma* sp.	
Centropages aucklandicus	*Scutellidium* sp.	
Gladioferans pectinatus	*Harpacticus* sp.	
Spicipes sp.		

Ostracoda:
Cladocera:
Daphnia carinata
Camptocercus sp.
Bosmina sp.
Simocephalus vetulus
Mysidacea:
Tenagomysis novaezealandiae
Natantia:
Paratya curvirostris
Isopoda:
Amphipoda:
Paracorophium sp.
Coelenterata:
Ctenophora:
Hydromedusae:
Anthomedusae:
Scyphomedusae:
Radiolaria:
Formanifera:
Ascidacea:
Oikopleura sp.

Many meroplankton forms were broadly classified into a general order or class. A general lack of published information on classification and identification of meroplankton forms makes identification difficult. Although barnacles were not identified to the species level they are most likely represented within the Brooklands Lagoon estuary by the species, *Elminius modestus*. The adult of this species has been recorded in the nearby Avon-Heathcote estuary and Lyttelton harbour and is commonly found throughout New Zealand on any hard surface in sheltered situations. This species is more able to withstand reduced salinities and the more sheltered aspect of settlement sites within Brooklands Lagoon than other marine species.

Many polychaete larvae, although obviously different were simply combined for analysis purposes. Identification of rare species to a specific level would have resulted in disproportionate weighting of data during statistical analysis because of their low numbers.

Copepod nauplii were also grouped together. Although literature is available the time necessary to accurately identify many different species in this group was not justifiable. Species within this group could be separated in retrospect by matching pulses in numbers of the adults with previous peaks in nauplii numbers.

Brachyuran zoeae were another group that was only tentatively identified to species. This group was probably represented by a single species, *Macrophthalmus hirtipes*, which is the common mud crab within the margins of Brooklands Lagoon. During the summer thirty-six hour survey megalopae of *Macrophthalamus hirtipes* were positively identified. Anomuran zoeae were almost completely absent, but a few zoeae of *Petrolisthes elongatus* were counted in January and August.

The infrequent occurrence is strange, as the species is commonly reported from the near-by Avon-Heathcote estuary and Lyttelton harbour environs.

Molluscan veligers were separated into two categories broadly classified as Gastropoda and bivalves. Gastropod types undoubtedly include *Amphibola crenata*, the common adult mud snail found at mid-tide levels around the estuary. However another common species appears as a very tiny veliger, with an appparently much more opaque shell. This species may be the very common *Potamopyrgus novaezealandiae*, which has an undescribed early life history.

In the present study, as in many previous, copepods were the most common holoplankton representatives (see Raymont 1983 for review). The species recorded in Table 1, are mainly neritic species. None of these were found outside their normal distribution range (Table 2).

The most commonly found copepods were *Acartia* species, which are common to the colder seas of the North Atlantic coastal waters. These shallow water species are euryhaline and commonly recorded in the estuaries of the northern hemisphere (Jeffries 1962a).

Oithona similis is a cosmopolitan, cyclopoid copepod. This species is especially common in the higher latitudes, with a recorded temperature range of -1°C-25°C (Table 2). Another cosmopolitan species found frequently in this study was the harpacticoid copepod *Euterpina acutifrons*. This is another euryhaline species which is well known from tropical seas and may be carried to temperate regions by currents (Raymont 1983, Moreira et. al. 1982). *E. acutifrons* may be abundant in waters of reduced salinity in late summer and autumn while temperatures are relatively high.

The calanoid family Centropagidae was represented in this study by two species, which were the only known carnivorous copepods. *Centropages aucklandicus* is very similar to *C. furcatus* of the northern hemisphere. *C. aucklandicus* is a surface dwelling, neritic species of temperate waters (Bradford 1978) widely distributed throughout the Pacific (Vervoort 1965). It was the largest copepod found in the present study. The second member of the Centropagidae was *Gladioferans pectinatus*. This is a euryhaline, estuarine species. It has been shown to be able to maintain station within estuarine waters by vertical migration (Bayly 1963).

Table 2. Species habitat range and distribution.

Species	Distribution	Lattitude	Tolerance Temperature	Breeding Temperature	Reference
Acartia clausi	North Atlantic		0-24°C	3-20°C	Farran 1948
Acartia tonsa	Temperate seas				
Paracalanus indicus		44-30°S	1-32°C	6-32°C	Colebrook 1964
Temora turbinata	Neritic, Top 50m,	50-35°S	0-22°C	3-20°C	Colebrook 1964
Centropages aucklandicus	Neritic,	50-35°C	-1.74-24°C	-1-20°C	Bradford 1978
Gladioferans pectinatus	Estuaries				Bayly 1965
Euterpina acutifrons	Neritic,	40-30°S	5-32°C	15-32°C	Deevey 1960b
Oithona similis		50-35°S	-1-25°C	-1-20°C	Colebrook 1964

Many more specifically marine life history stages appear rarely as members of the estuarine zooplankton. These taxa included the Ctenophora, leptomeduase, anthomedusae, scyphomedusae and ascidian larvae. Rare marine taxa are usually only able to enter the lagoon on high tides at periods of low river flow. At other times these taxa, especially the large coelenterates, become broken apart by wave action in the surf of the Waimakariri River mouth. Equally important were the obvious marine omissions from the zooplankton of the estuary. These included many open water species such as the

chaetognaths, salps, and doliolids. Many larger copepods were also absent from this environment, for example *Calanus* sp., and *Corycaeus* sp., both cosmopolitan carnivores.

The freshwater species are included in Table 1. These include the mysid *Tenagomysis novaezealandiae*, the natant decapod *Paratya curvirostris* a cyclopoid copepod *Microcyclops* sp. and the Cladocera: *Daphnia carinata*, *Camptocercus* sp., *Bosmina* sp. and *Simocephalus vetulus*.

SEASONAL TAXA DIVERSITY

A total of 48 taxa were recorded during the seasonal zooplankton survey. This list (Table 1) was reduced to 43 for analysis by eliminating 5 rarer species. The rare species included brachyuran megalopae found at sites two and three during May, and anomuran zoeae were present during August at site one, and at sites two and three in January. Euphausiid calyptopis and nauplii were only found at sites two and three during August and Phoronid actinotroch larvae at site one during December 1985 and October 1986. The calanoid copepod *Spicipes* sp. was only counted once during April at site one. Another copepod, *Harpacticus* sp., was only found at sites two and three during December 1985.

SITE ONE

Site one had the highest recorded number of taxa amongst the three sites in Brooklands Lagoon (Fig. 3). A total of 40 taxa were found at this site during the yearly survey. However not all taxa were present in the same sampling period and taxa diversity ranged from 11 during February to 24 during May and July. This site consistently had the lowest monthly taxa diversity. Several of the

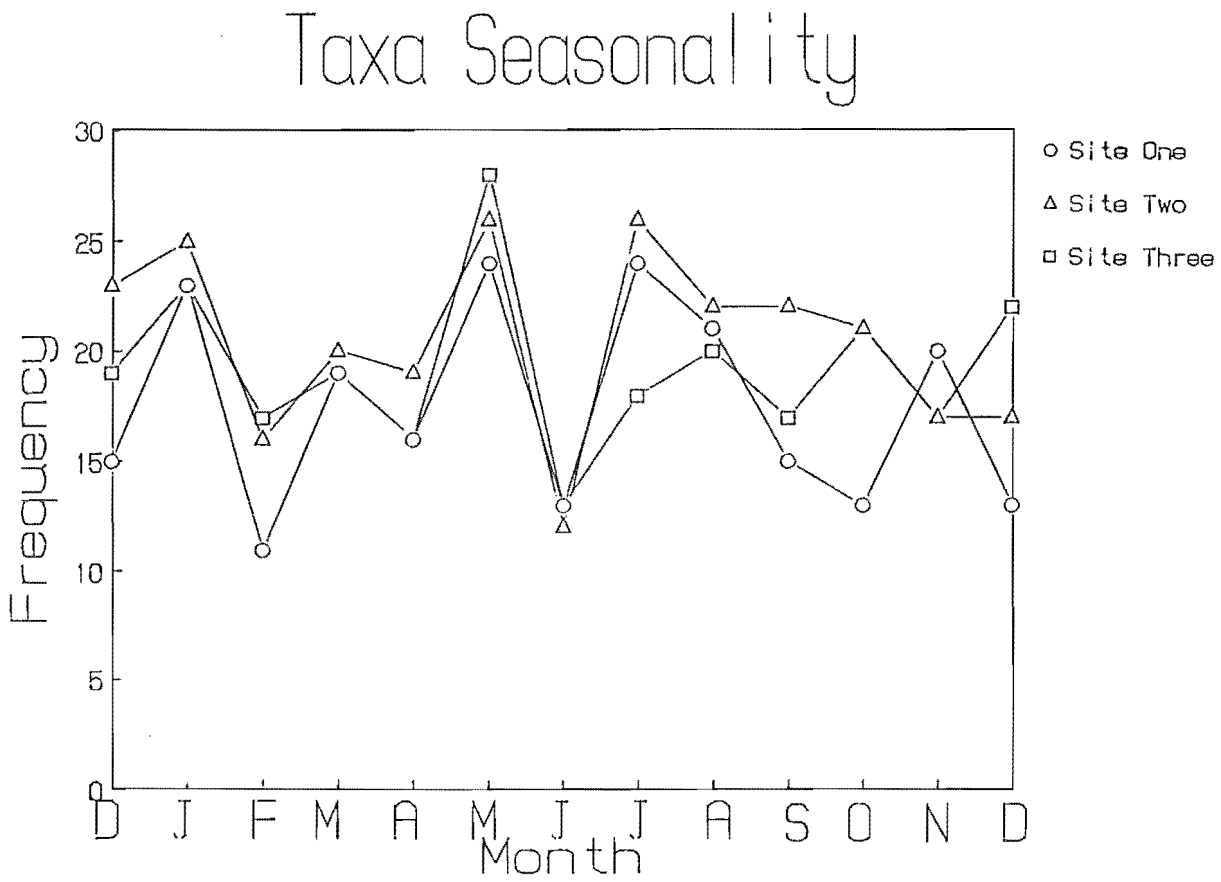


Fig. 3 Total number of taxa recorded form each sample site from December 1985 to December 1986.

taxa showed distinct seasonal appearances. During June and February taxa numbers were very low while very high taxa diversities occurred during January, May and July.

The most obvious feature of site one was the presence of a wide variety of freshwater species. Important amongst these were the Cladocera which are represented by four species, *Bosmina* sp., *Simocephalus vetulus*, *Daphnia carinata* and *Camptocercus* sp. There was a reduction in the numbers of harpacticoid copepods present with only two representatives, *Euterpina acutifrons*, a coastal species and *Miscegenus heretunga*, a more numerous and active meiobenthic copepod.

Many marine taxa exhibited very patchy seasonal distributions at site one. These species included the normally more abundant calanoid copepods such as *Paracalanus indicus*, *Centropages aucklandicus* and *Temora turbinata*. The absence of these species tended to depress the taxa diversity. Many of the smallest meroplankton were present throughout the year. Barnacle nauplii were absent during Decemeber 1985, June, September and October. Copepod nauplii were absent in February and enteropneust tornaria larvae were absent in October. Larger species such as the copepods *Centropages aucklandicus*, *Temora turbinata* and *Paracalanus indicus* show periodic appearances throughout the year.

SITE TWO

Site two had 39 recorded taxa types, but it had the greatest monthly diversity of species (Fig. 3). The highest monthly diversity of taxa (26) was recorded in May and July. The lowest diversity occurred in June (12). The taxa found at this site included a larger

proportion of coastal and euryhaline estuarine resident groups. Fluctuations in the numbers of taxa present at site two occur at similar periods of the year to site one.

The larger, coastal species, *Paracalanus indicus* and *Oithona similis*, showed less patchiness in seasonal distribution at site two. There were reduced occurrences of freshwater species with only two cladocerans, *Daphnia carinata* and *Camptocercus* sp., found. The large, calanoid copepod of freshwater origin, *Gladioferans pectinatus*, was never found at site two, which however did include the more euryhaline Cumacea.

Some taxa at site two maintained a continuous presence throughout the year. These included barnacle cyprids, copepod nauplii, *Acartia* sp. copepodites and *Miscegenus heretunga*.

SITE THREE

Site three had the lowest number of taxa of all sites (37 taxa) but in general had a higher monthly diversity than site one (Fig. 3). The lowest taxa diversity occurred in June (13). This was due to the seasonal appearance of resident estuarine copepods such as *Quinquelaophonte* sp. and *Halectinosoma* coinciding with the appearance of rarer coastal taxa. These taxa included ascidian larvae and ctenophores. The species composition was similar to site two with fewer freshwater zooplankton occurring. Mysids appeared in only three out of the 13 months at site three and *Bosmina* was not found here. Although three cladocerans were found at site three *Simocephalus vetulus* was very rare and *Camptocercus* sp. was patchily distributed through all seasons. Larger taxa such as medusae were also very rare at this site, which is furthest from the sea. Site three contained four taxa which were consistently present in the plankton. These were barnacle cyprids, copepod nauplii, *Miscegenus heretunga* and

Acartia sp. These were the same groups that were regularly present at site one. Some other groups also had a more sustained appearance through the year at site three. These included the bivalve and gastropod veligers and enteropneust tornaria larvae. During May and December 1985, site three had the greatest monthly diversity of the three sites (28).

SEASONAL PATTERNS OF DIVERSITY

Throughout the year all three sampling sites showed similar changes in the number of taxa present (Fig. 3). They all showed the greatest number of taxa present during May, at the end of autumn when the average abundance was 21.1 taxa. July had the lowest numbers of taxa during the year with an average of 12.7 taxa. Winter was the season of greatest changes in taxa diversity throughout the estuary. The highest and lowest monthly diversities were recorded during the consecutive months of May (26) and June (12.7). This effect is, however, hidden in the seasonal averages. When the results were combined to look for seasonal variations fewer differences were seen between sites and times of year (Table 2).

The seasonal average taxa numbers at each site are shown in Table 3. The overall pattern shows site one has the greatest fluctuations in taxa diversity between seasons and this was most likely due to flood events in the Waimakariri River. Site two appeared the most stable with no significant differences in taxa abundance between any season. This effect was probably due to a buffering effect of species replacement at this site from less variable coastal sources. Site three, like site one, showed a larger range of taxa numbers. The fluctuations at this site may be due to a more thorough mixing of water masses at this site, introducing some

of the variability from site one. Seasonal taxa averages showed the lowest diversities present during summer and spring when total zooplankton abundances were greatest.

Table 3. Average number of taxa per site.

Site	Summer	Autumn	Winter	Spring	Average
One	15.0	20.0	19.3	16.7	17.7
Two	20.5	20.7	20.7	21.0	20.7
Three	20.5	21.3	17.7	19.0	19.6
Average	18.7	21.1	19.2	18.9	---

DISCUSSION

Miscegenus heretunga which was recently described by Wells, Hicks and Coull (1982), is a major component of the meiobenthos from shallow harbours and estuaries throughout New Zealand. Several difficulties were posed to these workers when they were establishing the etymology of this species, mainly due to its intermediate nature *M. heretunga* cannot be accommodated within the known genera of the Diosaccidae.

Miscegenus heretunga has been recorded from several localities throughout New Zealand, ranging from Otago Harbour in Southland to Whangateau Harbour in Northland. *M. heretunga* is common to fine silty sand substrates in the headwaters of estuaries and the lowest reaches of many rivers, where salinity is reduced by freshwater flows, such as site three at Brooklands Lagoon. Previous reports show this species constituting up to 33% of copepod numbers from benthic samples (Hicks pers. comm.), but where species diversity increased numbers of *M. heretunga* tended to decrease. These two trends are both evident from my own collections at Brooklands Lagoon.

M. heretunga has not been previously recorded in New Zealand in plankton samples. My samples nearly all include some representation of *M. heretunga* which cannot be due to collections being made from

close to the benthos surface. All plankton tows were made in the surface water at high tide in 1.5m to 2.5m of water. This evidence could explain some of the difficulties encountered describing the intermediate nature of the etymology of this species possibly due to structural adaptations for a planktonic phase.

TAXA DIVERSITY

Brooklands Lagoon estuary has a relatively depressed zooplankton fauna. Although nearly all the major zooplankton taxa were found several major marine groups were lacking. Chaetognaths, adult Euphausiacea, salps and Doliolids were absent. Absences within the zooplankton fauna are less obvious at a lower taxonomic level, for example Formanifera. Many taxa were represented by few species. Occurrences of many other taxa were sporadic and appeared only during the calmest weather. This coincided with low river flow which is directly affected by alpine weather patterns. Movement of these groups can only occur in calm weather, especially the larger medusae and salps as their fragile structure is often destroyed in the surf (Bougis 1971). Intermittant appearances of hydroid medusae, ctenophores, ascidians, isopods, amphipods and ostracods from marine and coastal origins (Bary 1959, Bougis 1976, Grieve 1966) are probably affected by access through the Waimakariri River mouth.

Some groups that occurred in Brooklands Lagoon were represented by a small fraction of their common species, which are normally quite diverse in marine waters. These groups were the calanoid copepods, brachyuran larvae and cirripede larvae. For example, although calanoid copepods were at times very abundant, only seven species were identified in Brooklands Lagoon compared to 19 found in the Avon-Heathcote rivers estuary (Roper et. al. 1983), thirteen commonly found by Grieve (1966) at Kaikoura and twenty from the Hauraki gulf

(Jillet 1971). Other groups with low diversity were the barnacle nauplii which were represented by *Elminius modestus*. Similarly brachyuran larvae were represented by a single species *Macrophthalamus hirtipes*.

Zooplankton species lists obtained for Brooklands Lagoon compare poorly with similar studies of marine zooplankton elsewhere in New Zealand. For example Roper et. al. (1984) found 93 taxa in the Avon-Heathcote estuary during a six month survey. Other studies in New Zealand have all been made in coastal and shelf waters. These all showed taxa counts higher than that found for Brooklands lagoon. Jillett (1969) found 94 taxa in the Hauraki gulf and Grieve (1966) found 64 taxa at Kaikoura (Table 4).

Table 4 : Comparison of zooplankton species diversity.

				Species Origins			Copepods Origins				Total
Origin	Author	Year	Habitat	Mar.	Est.	F.W.	Mar.	Est.	F.W.	Total	Zooplankton
Africa	Dumont	1986	River	0	0	78	0	0	40	40	78
Antarctica	Miller	1985	Coastal	69	0	0					69
Arctic	Evans and Grainger	1980	Estuary	28	4	8	8	1	4	13	40
Aust.	Bayly	1963	Estuary	8	4	4	8	4	4	16	16
Aust.	Kimmerer and McKinnon	1985	Coastal	33	17	0	40	0	0	40	50
Aust.	Shiel	1986	River	0	0	200	0	0	27	27	200
Aust.	Shiel	1986	River	0	0	155	0	0	22	22	155
Canada	Sprules	1977	Lake	0	0	26					26
Canada	Mackas and Anderson	1986	Fjord	49	5	2	24	5	0	29	56
Canada	Redwood and Spules	1986	Lake	0	0	23	0	0	4	4	23
Japan	Madhuratap and Onbe	1986	Coastal	37	0	0	30	0	0	30	37
N.Z.	Bary	1959	Coastal	20	2	0					22
N.Z.	Cassie	1965	Coastal	Selected species							6
N.Z.	Wear	1965	Coastal								30
N.Z.	Grieve	1966	Coastal	58	6	0					64
N.Z.	Jillett	1971	Coastal	94	0	0	55	0	0	55	94
N.Z.	Jillett	1976	Coastal	37	0	0	15	0	0	15	37
N.Z.	Stout	1969	Lake	0	0	11	0	0	2	2	11
N.Z.	Knox and Kilner	1973	Estuary	Avon-Heathcote estuary macro-bentho							188
N.Z.	Knox and Bolton	1977	Estuary	Brooklands Lagoon macro-benthos							35
N.Z.	Roper et. al.	1982	Estuary	67	12	14	10	9	0	19	93
N.Z.	Present Study	1986	Estuary	21	18	7	10	7	1	18	46
U.S.A.	Deevey	1960	Estuary	88	16	0	47	7	0	54	103
U.S.A.	Yuh Lee and McAlice	1979	Estuary	17	0	0	11	0	0	11	17.

Comparisons with other estuarine zooplankton communities must be made with studies in other countries. Deevey (1960a) counted 103 taxa excluding the meroplankton in Delaware Bay. This area, on the eastern seaboard of the U.S.A., represents a region several times larger than Brooklands Lagoon. Delaware Bay water is always well mixed at all stages of the tidal cycle and can be expected to contain a much larger representation of marine species. It had a very poor representation of freshwater species. Even without this component it still has many more taxa than Brooklands or any other New Zealand coastal record. Evans and Grainger (1980) found 40 taxa in a Canadian arctic estuary, which is closer in size to Brooklands Lagoon. However their study was carried out in a single month and many rarer and out-of-season species may have been missed from this survey. Bayly (1963) found 16 common copepod species in an Australian river tidal reach, which can be considered an estuary. Here the river dominates this system even more than the Waimakariri River dominates Brooklands Lagoon. Mackas and Anderson (1986) counted 56 taxa in a British Columbian fjord which only had two freshwater species despite a sizable river emptying into this basin. Miller (1985) found 69 zooplankters living in the lee of some sub-antarctic islands. In this offshore study there were no species present which had previously been recorded from estuarine or freshwater situations.

These comparisons show that marine fauna is far more diverse than shallow water estuarine communities. This influence can extend into shallow water depending on the depth and degree of water mass mixing. Estuarine systems with a large freshwater flow tend to have less diverse fauna. This suggests that the downhill river flow may be pushing the tide out of the estuary, or preventing it from entering. This means that coastal water entering an estuary must be pushed uphill by the rising tide (Heath R.A. 1987 pers. comm.)

With a very large freshwater flow entering an estuary, a reasonable expectation could be the replacement of marine fauna with normally more freshwater tolerant species. This phenomena does occur to some degree, but most freshwater species are stenohaline. For example, Evans and Grainger (1980) found 8 freshwater taxa, Roper et. al. (1983) counted 14 freshwater taxa, Bayly (1964) counted 4 freshwater taxa and Sprules (1977) counted 26 common species of zooplankton in a Canadian shield lake. Comparisons with the freshwater components of other ecosystems show that freshwater zooplankton are less diverse than marine zooplankton. This trend is illustrated by Sprules (1977) who found 26 common species of zooplankton in Canadian shield lakes. Stout (1969) found 11 species of zooplankton common to Lakes Pearson and Grasmere in the upper catchment of the Waimakariri river. This could mean that even with the replacement of marine taxa with freshwater species within an estuary, taxa diversity would always be less than in a nearby marine community.

Even though Brooklands Lagoon has a much larger freshwater inflow than the nearby Avon-Heathcote estuary, the very low zooplankton diversity cannot be accounted for by this difference alone. The Brooklands lagoon estuary is approximately a third of the size of the Avon-Heathcote estuary. This factor could be expected to effectively depress the abundance of zooplankton, but not necessarily the diversity. Knox and Bolton (1977) found 35 macro-benthic species in Brooklands Lagoon compared with 188 found in the Avon-Heathcote estuary (Knox and Kilner 1973). Knox and Bolton attributed this difference to the influence of man, and later found that Brooklands Lagoon had a very high coliform count.

On the receding tide there was a sharp decline in the average number of taxa found within Brooklands Lagoon. The most notable absences during these periods were ascidean larvae, Ctenophora, *Daphnia carinata* and *Simocephalus vetulus*. These taxa are all outside their normal salinity preference range within the estuary. Ctenophores may have been broken apart by water mass mixing within the estuary, while *Daphnia carinata* and *Simnocephalus vetulus* have behavioural mechanisms to avoid more saline conditions of receding tidal flows. Other taxa absences appear to be due to prevailing light conditions coinciding with low tide and darkness.

CONCLUSIONS

Many studies recognise the usefulness of plankton species as indicators of water movement and hydrological conditions (Jeffries 1962, Bougis 1976, Bradford 1977, Hardy 1970, Van derSpoel and Hayman 1983). Evidence for New Zealand's position within the sub-tropical convergence zone is provided by the presence of a temperate species, *Euterpina acutifrons* within Brooklands Lagoon. This species has been carried south by the East Cape Current and mixed with water from the sub-Antarctic. Carried north by the Southland current water from the sub-Antarctic are species such as *Oithona similis* and *Temora turbinata*.

The estuary itself is a zone of active mixing water masses between waters from terrestial runoff and coastal marine origins. This process can be illustrated by the presence of freshwater indicator species such as *Daphnia carinata* and *Microcyclops* sp. in the same water samples as *Acartia* sp. and *Oithona similis*, which are indicators of marine waters.

In conclusion, several species found in estuaries such as *Daphnia carinata*, *Microcyclops* sp., *Acartia* sp., *Oithona similis*, *Euterpina acutifrons* and *Temora turbinata* may be used as indicators of water origins and hydrographic conditions within estuaries.

CHAPTER TWO

ZOOPLANKTON SEASONAL SURVEY

INTRODUCTION

In temperate regions, zooplankton normally show seasonal cycles with greatest densities of species during the warmer times of the year. These cycles are usually dominated by the breeding cycles of holoplankton, especially the copepods (Deevey 1960a). Individual species show peak densities at different times of the year related to their life history characteristics, the locality and its physico-chemical characteristics (Raymont 1983).

Species in southern latitudes have been shown to follow the annual cycle of phytoplankton production. However the colder temperatures at these latitudes slows metabolism of these species causing a lag effect in the cycles of abundance compared with the phytoplankton (Voronia 1970). Food supply is seldom the only factor necessary for favourable reproductive conditions. Food concentrations photoperiod and temperature are also important for some species. These factors may in turn reflect local hydrological conditions such as upwellings, gyres and storm fronts. Such areas are common centres for high zooplankton production and abundance (Tranter et. al. 1983a, 1983b, Bradford 1985).

In general the total zooplankton maximum abundances in summer may be seven to ten times higher than winter abundances (Hopkins 1977). Moore (1949) showed similar seasonal patterns of abundance but found that peaks also occured in spring. Deevey and Brooks (1971) showed peaks in spring and autumn following phytoplankton bursts of abundance in the Sargasso Sea.

Zooplankton of inshore areas show greater seasonal fluctuations of abundance and composition than nearby shelf and oceanic waters (Cushing 1975). Seasonal fluctuations in zooplankton production also increase in the higher latitudes. Seasonal fluctuations of abundance are common in shallow coastal waters of the temperate latitudes. Fluctuations usually have a single peak in spring; one to three during summer and another during autumn. During winter, populations drop to minimum maintenance levels (Raymont 1983).

Zooplankton studies on shallow coastal waters have shown that the numbers of holoplankton species markedly dominate the seasonal total zooplankton changes. This contrasts with the meroplankton where larval release tends to cause short intense peaks in zooplankton abundance (Raymont 1983).

This study investigates seasonal abundances of both the holoplankton and meroplankton from an estuary influenced by river flow and coastal waters. In such shallow areas marked fluctuations of the weather and environmental factors tend to produce larger seasonal breeding fluctuations of marine species (Barnes 1974). Other studies have shown that most of the species in the benthos, and the fish, reproduce in spring and summer (Odum 1971, Barnes 1974). Species which have planktonic stages appear in the meroplankton during spring and summer. Barnacle nauplii appear in greater abundance in the spring, pluteus, tornaria and fish eggs have peak abundances in the spring to summer time. Medusae have peak abundances in autumn and bivalve larvae peak in summer, while annelid larvae have peak abundances in late winter (Raymont 1983). Some benthic invertebrates exhibit lunar periodicity in the release of larvae or gametes and may totally dominate the zooplankton for a short time.

The most well known example of this occurence is the release of the Palolo worm epitoke during the summer equinox in the islands of the South Pacific (Fauvel et. al 1959).

The aims of this part of the study are to examine differences in the zooplankton between Brooklands Lagoon and other estuaries and coastal waters. The three sites previously described (Chapter 1) were used for the seasonal study and an attempt has been made to relate the densities of species to the physico-chemical variables.

Community analysis will describe the patterns of abundance and distribution. Using cluster analysis samples may be classified by species abundance, highlighting differences in distribution along the length of the estuary and through the seasons. Bray-Curtis ordination will be used to correlate the physico-chemical parameters with observed abundances. The aim of this section of the study is to explain the causes of observed species abundance fluctuations within the estuary during each season in relation to the measured variables. Bray-Curtis ordination and Principle Components analysis have been used successfully in the past by a number of workers to indicate species habitats and causes of distribution patterns.

METHODS

Field Sampling

Field sampling was carried out using the same monthly survey that was described in chapter one. Samples collected were also analysed for numbers of individuals of different species each within the estuary as described in the laboratory procedures in chapter one.

During each trawl, water samples were taken for later analysis in the laboratory for oxygen concentration and chlorophyll a concentration. Oxygen samples were fixed in the field by addition of Winklers reagents, ~~manganese dioxide~~ Manganous chloride OR $MnSO_4$ and sulphuric acid. These were

removed to the laboratory for titration with sodium thiosulphate. Chlorophyll a concentration determinations were made using acetone extraction for spectrophotometer readings. During each trawl the temperature was measured using a mercury thermometer and chlorinity was measured using a hand-held Atago meter. Chlorinity readings were later converted directly to salinity measures using the formula SALINITY = 0.03 + (1.805 * CHLORINITY) (Davis 1955), which was adjusted according to temperature readings. Waimakariri river flow data was collected for the periods of the zooplankton trawls, from the permanent hydrographic station of the North Canterbury Catchment Board at the old State Highway One bridge. This data was averaged on a weekly basis. Furthermore days where river flow inreases of more than one third of the previous day were counted as river floods. Visibility was measured using a hand held secchi disk and readings were subtracted from the greatest visibility depth to obtain a turbidity measure.

All tows were made in the opposite direction of the tidal flow and in the same time period of the tidal cycle in an effort to reduce the variance within each sample. In most cases this method and the effects of averaging fifteen subsamples significantly reduced experimental variance.

Statistical Analysis

Results from the three sub-samples were averaged to provide an estimate of the plankton species abundances from each trawl. The estimates from each trawl were in turn averaged to provide estimates of the zooplankton species at each site for each month. Yearly averages for the three sites and monthly averages for the whole estuary system were used for graphical analysis. A more detailed analysis using Bray-Curtis multivariate ordination was performed on

data separated into separate month and site values and overlayed with physico-chemical data values. Other variables used in the statistical analysis were the distances of the three collection sites from the sea; the height of the tide on the days collections were made and the time of the day. A preliminary examination of the data collected highlighted several species that were very rare in occurrence such as the polychaete actinotroch larvae. Other more abundant species such as barnacle nauplii were occasionally recorded in concentrations as high as 26,000 per litre. Species occuring only once at a single site in a single month were eliminated from the working data set and excessive weighting effects of rarer species were eliminated by logarithmically transforming the data set which still maintained the assumptions of normality.

Although it is not possible to describe environmental cause and effect with any more certainty with a particular data set, more sophisticated analytical techniques are available to clarify and separate factor effects within the data. These techniques are recommended by Cassie (1960), because of the complex interactions between physical variables in seasonal and spatial dimensions on species abundance and distribution patterns. Basic patterns of distribution and causes of abundance of single species are already well known in many instances, but further analysis has often highlighted potential indicator species. These species are often useful indicators of existing environmental conditons and water mass origins.

Cluster analysis produces clusters of samples in theoretical n-dimensional space. Clusters are based on species presence and abundance in common, between the samples accounting for as much sample variance as possible. Successive dimensions are based on residual variance from the previous dimensions, attemptting to

explain as much variance as possible. Samples in the same cluster all have similar variance, and by association similar ecological factor causes. For example, factors such as the time of year, geographical position, time of day the sample was taken or the height of the tide or volume of freshwater flow could all, separately or in combination, be the major cause of species distribution patterns.

Bray-Curtis ordination techniques were used in this analysis which aligns species and samples along hypothetical dimensions based on size of sample variance. The vectors for each dimension can then be correlated with environmental variables measured with each zooplankton sample. These correlations will highlight the most likely influencing environmental variable that was measured. In most estuarine studies the main environmental variables have been those of temperature, salinity and river flow. Alternatively this analysis may show that some other unsuspected and unmmeasured variable may be the controlling factor within the environment. The degree of correlation between measured factors and computed vectors often gives clues to the type of variable that should be measured to show the real cause and effect of species patchiness.

RESULTS

Physical and Chemical Parameters

Average values for several physical and chemical variables at the time of zooplankton trawls are shown in Figures 4-8 including river flow measured at one location where the Waimakariri River flows past the mouth of the estuary.

The readings for the river flow are shown in Figure 4 and are a good indication of the preceding weeks rainfall in the mountains. In general there was an autumn decrease and a spring increase in river flow. The lowest flow periods were in mid summer and early winter,

that is January and May respectively. During the year river flow had many separate flood events. These tend to be obscured by the average weekly values plotted for the sample periods in Figure 6. There were an average 3 floods each month when river flow increased over the preceding day (Fig. 4).

Water temperature follows a standard annual cycle (Fig. 5). From its highest values in mid summer, water temperature decreased relatively uniformly through autumn and reached its lowest values in mid winter during July. With the appraoch of spring the air temperature increased, closely followed by a similar change in the water temperatures. Each month the temperatures at all three sites were not more than two degrees of each other and were not significantly different when tested by either Chi-square or by ANOVA. $P=0.005$ $Fs[2,36]=0.0047$.

Salinity in the estuary was generally similar throughout the year (Fig. 6). All three sites within the estuary receive water of a low salinity throughout the year. values below 5 ppt. were consistently recorded at site one which was in the Waimakariri River. During January and June in 1986 two periods of high salinity were recorded at all sites. However site 3 showed higher concentrations with values upto 50% normal seawater. These months appear to coincide with periods of low river flow. Due to temperature differences dissolved oxygen concentrations have been converted to percentage saturation as a means of comparison (Table 5).

Fig. 4 Flow volume and flood frequency of the Waimakariri River from December 1985 to December 1986.

Fig. 5 Temperature at each sample site within Brooklands Lagoon from December 1985 to December 1986.

Fig. 6 Salinity at each sample site within Brooklands Lagoon from December 1985 to December 1986.

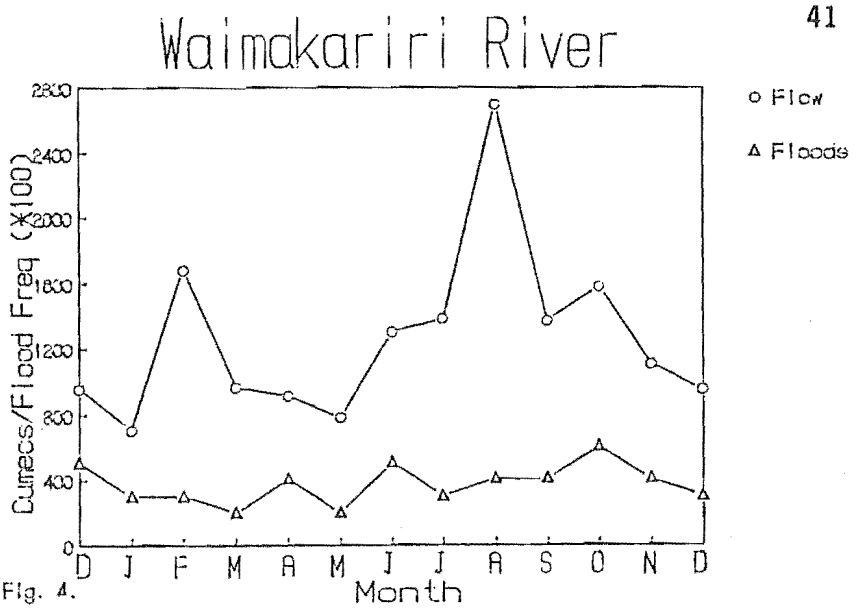


Fig. 4.

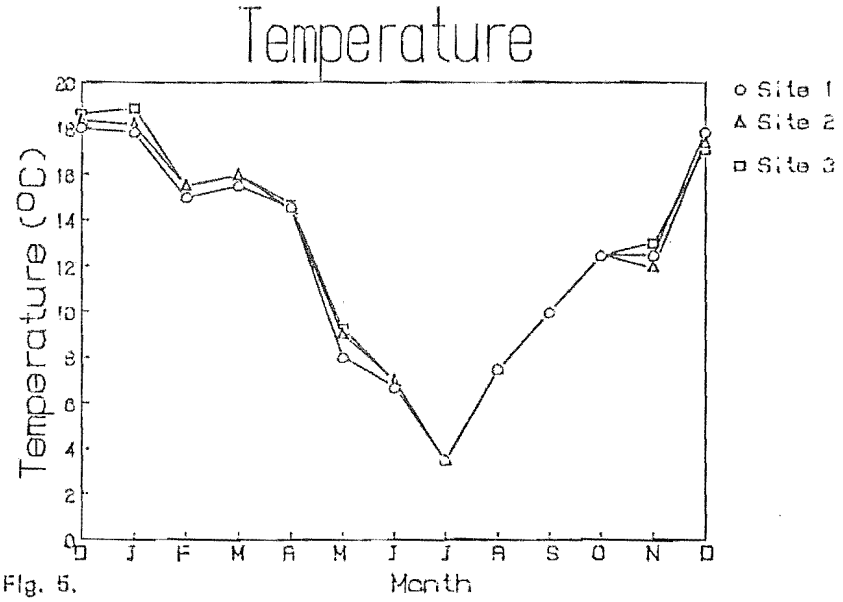


Fig. 5.

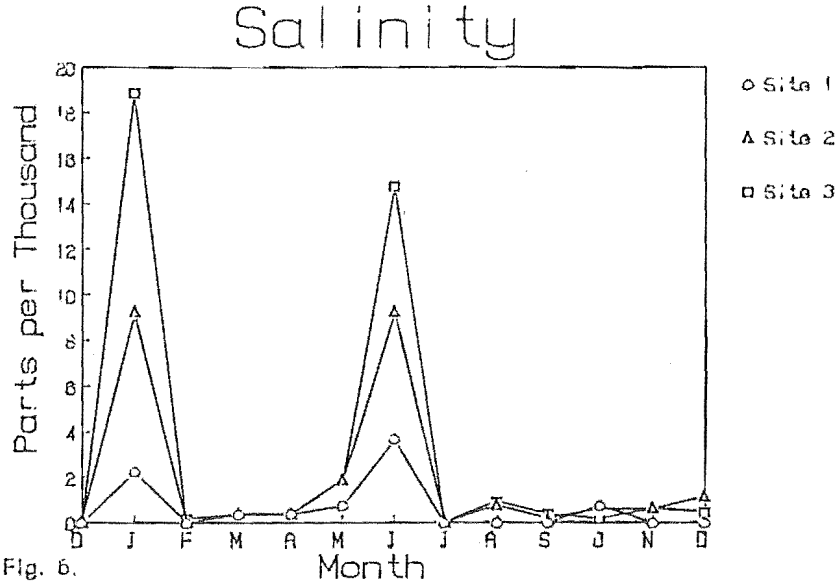


Fig. 6.

TABLE 5. Percentage Dissolved Oxygen Concentrations in Brooklands Lagoon.

Month	S1	S2	S3
Dec	86.78	95.37	100.00
Jan	30.10	50.00	100.00
Feb	100.00	85.94	82.81
Mar	73.85	100.00	99.99
Apr	46.19	100.00	90.72
May	100.00	60.00	85.33
Jun	100.00	97.30	97.30
Jul	100.00	83.33	51.61
Aug	100.00	97.00	91.66
Sep	96.18	100.00	98.82
Oct	91.40	98.92	100.00
Nov	93.71	100.00	95.80
Dec	100.00	97.14	100.00

During the year oxygen readings were all high compared to readings from the lower Waimakariri River (Winterbourn et. al. 1971). Low values were recorded in January at the same time as high zooplankton abundances, low river flows, two floods and high salinities. Similarly low values were recorded during April and July which coincided with higher zooplankton abundances at these sites. At these times there were also high chlorophyll a concentrations.

Measures of turbidity correspond to the inverse of water clarity. This means that clear water produced low turbidity readings (Fig. 7). The most turbid conditions occurred during February, March and July through to September and at this time river flow had its highest values as did river flooding. During these times direct observations showed that river floods completely flushed Brooklands Lagoon. Silt loadings from the river were deposited when the river water enters the slower backwaters of the estuary. Furthermore increased salinity occurring during high tide phases causes increased floculation of suspended organic and sediment particles (Mclusky 1971). This event drastically depresses the water clarity. Although site one was in the river it was often clearest as the force of the river flow pushed the seawater interface and thus the area of most

floculation, further towards the river mouth. During low river flows Waimakariri water sources derive from spring and lakes. These are both clear, cold sources with low zooplankton abundances, high clarity and low turbidity.

Chlorophyll a concentrations (Fig. 8) fluctuated widely at all three sites with no obvious pattern of oscillations. Further no one site exhibited a consistently higher average reading. The highest values were recorded at site one, the river site, but these dropped to zero at times. The lowest overall values were recorded in July at all three sites. These readings coincide with the period of the lowest water temperatures. Low readings also occurred during October and February. Because of widely fluctuating chlorophyll a concentrations found between the sites, there is no evidence for general phytoplankton blooms in the estuary. Blooms may however be the cause of the fluctuations in chlorophyll a readings at each individual site.

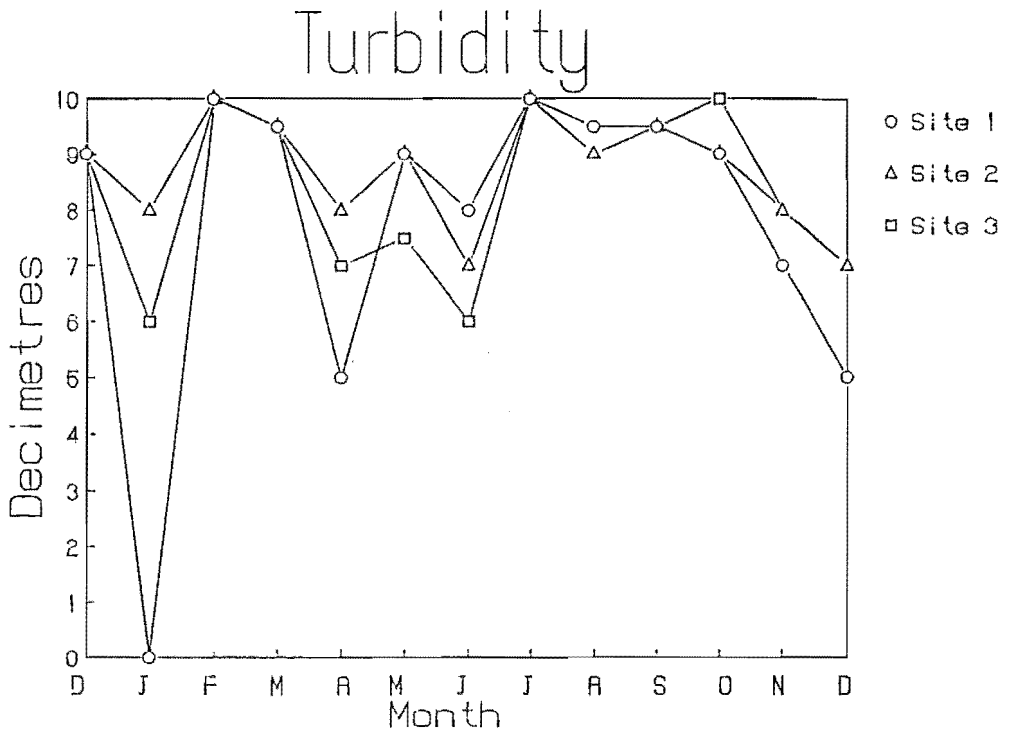


Fig. 7 Turbidity at each sample site within Brooklands Lagoon from December 1985 to December 1986, as inverted seechi disc readings.

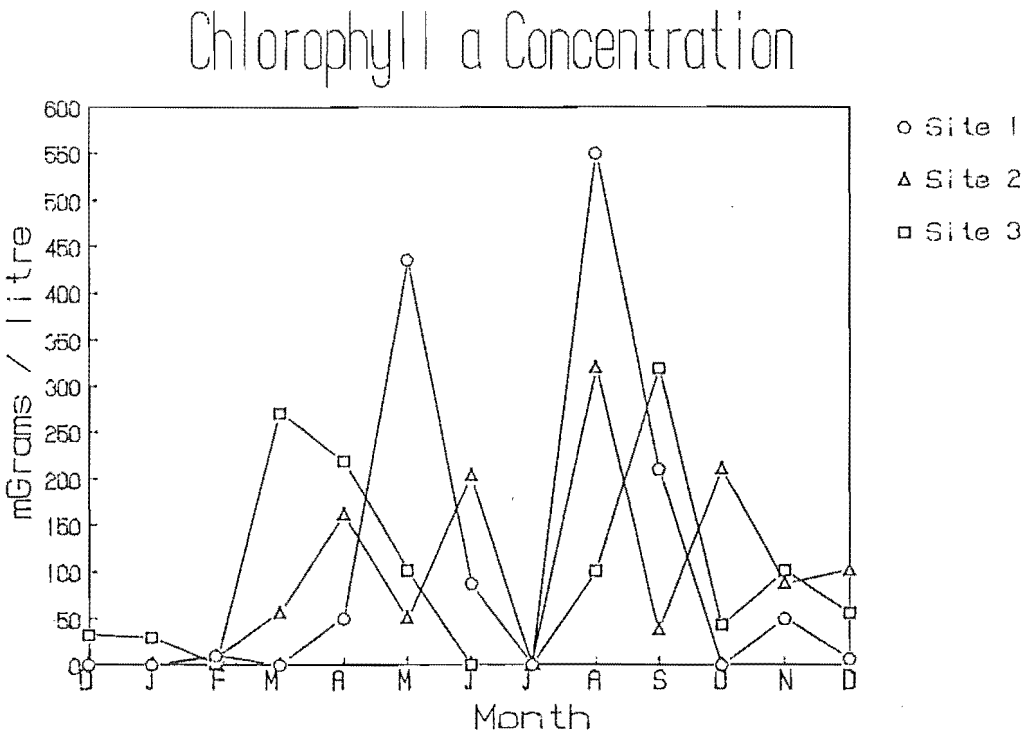


Fig. 8 Chlorophyll a concentration at each sample site within Brooklands Lagoon from December 1985 to December 1986.

TAXA ABUNDANCES

General abundances

For Brooklands Lagoon there were similar fluctuations of total zooplankton abundances at the three sites (Fig. 9). Total numbers of zooplankton increased during summer reaching peak densities in January. During January temperatures were also highest. Over the next two months there was a steady decline in numbers, until April, after which there was a second increase in abundance. In June, at the start of winter, there was a sharp drop in numbers coinciding with the coldest period of the year. This was followed by a rapid return to high densities in August and then a general decline in numbers from September until the end of spring, in November. At this time abundances increased again and the zooplankton abundance repeated at the previous summer.

Most species showed lowest abundances at site one. However Figure 9 masks this effect because of the logarithmic scale. At site one densities were usually an order of magnitude less than at site three and up to two orders of magnitude less than site two. The lowest abundances were nearly always recorded at site one.

Although total abundances varied with season at all three sites, species composition differed between sites. Inter-site differences are apparent in the proportional representation of common species. The taxa responsible for the main changes in total zooplankton abundances varied between seasons at the same site (Figs. 10-12).

Out of the 43 species used for analysis the number of numerically dominant taxa ranged from two to seven at each site. For example, in December 1985 there were five species recorded in the numerical dominance rankings at site one, two at site two and seven at site three. Generally site one had abundances of numerically

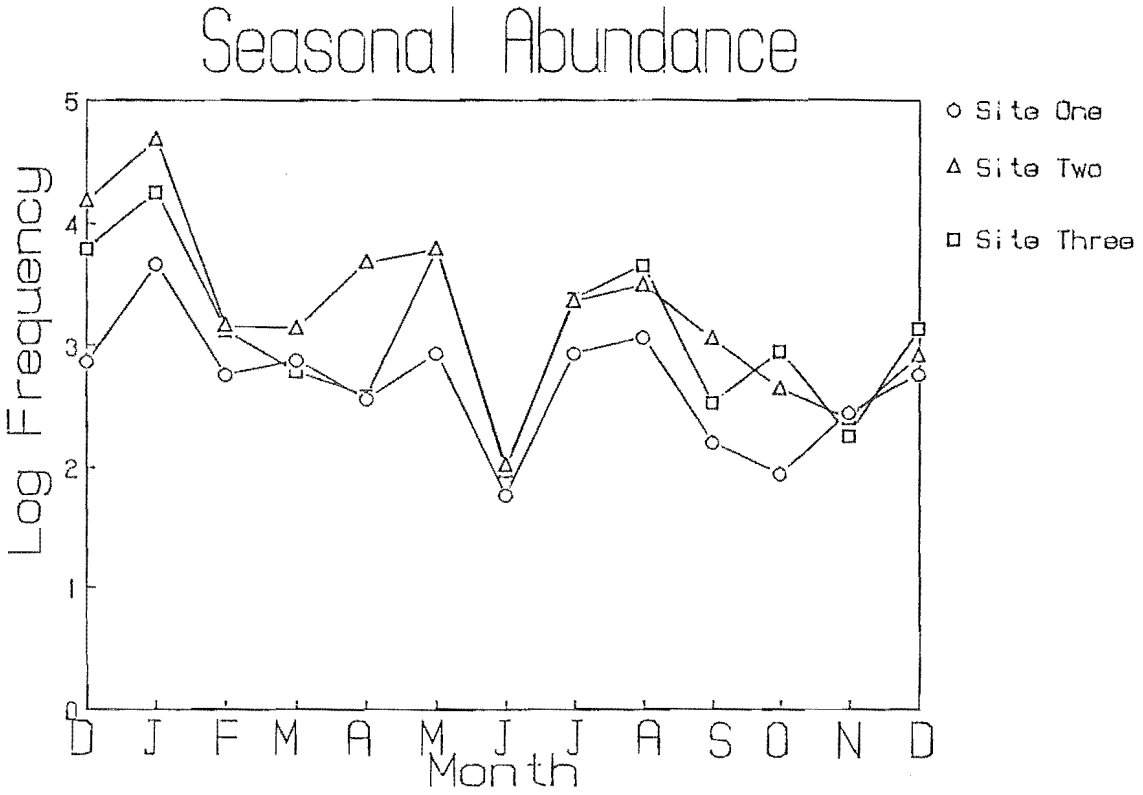


Fig. 9 Total zooplankton abundance at each sample site within Brooklands Lagoon from December 1985 to December 1986.

dominant taxa which differed from sites two and three. Some dominant taxa also showed different patterns of numerical dominance at site one from either of the two other sites.

Site One Abundances

The numerically dominant taxa changed at site one on a monthly basis. Some taxa densities reached much higher values than others. The number of taxa present in each month at site one varied from 11 to 24, only five taxa had numbers exceeding five pecent of the total taxa numbers in for any single month at site one (Fig. 10). There were 16 taxa in this category during the year from the total list of 48. At all three sites during the year there were 20 species abundances exceeding 5% of the total numbers. These were: barnacle nauplii, copepod nauplii, barnacle cyprids, tornaria larvae, gastropod veligers, bivalve veligers, brachyuran zoeae, *Acartia* sp., *Paracalanus indicus*, *Microcyclops* sp., *Temora turbinata*, *Euterpina acutifrons*, *Miscegenus heretunga*, *Daphnia carinata*, *Camptocercus* sp., *Quinquelaophonte* sp., *Paratya curvirostris*, Ostracoda and fish eggs. In Figure 11, numerically dominant taxa, constituting more than 5% of the total abundance each month, have been plotted as a proportion of the total taxa count including all species.

Copepod nauplii were abundant throughout the year and were generally the most numerous group at this site. Other groups were not numerically dominant for such long periods. For example, *Miscegenus heretunga* was dominant most of the year except for short periods during the winter, the end of summer and the end of autumn. Polychaete tornaria larvae became members of the dominant taxa intermittantly throughout the year. Fish eggs showed a seasonality of

appearance, and were the numerically dominant portion of the zooplankton during late summer (February) through to mid-winter (July).

A freshwater decapod, *Paratya curvirostris* was the numerically dominant species during spring and summer (October through December). A freshwater copepod *Microcyclops* sp. was also numerically dominant during spring from September through November, and was also dominant during March and June. Other brackish water species such as the mysid, *Tenagomysis* sp. show periodic appearances at site one but the numbers did not exceed five percent of the total abundance. Many taxa were included in this less abundant category, especially the larger coastal holoplankton such as the coelenterates and ascidians.

Some species appeared in greater abundance for brief periods. This group includes species generally associated with coastal waters. For example *Acartia* sp. occurred in December, January and August, and *Paracalanus indicus* in August. *Euterpina acutifrons* was more numerous in April, whereas *Temora turbinata* showed high densities in June.

Site Two Abundances

Fourteen species exceeded five percent of the total at some time at site two (Fig. 11). As in site one, several categories of abundance were observed. Some taxa such as *Acartia* sp., *Paracalanus indicus*, Tornaria larvae and barnacle nauplii had longer periods of high relative abundance. Estuarine species like *Miscegenus heretunga* had sporadic periods of numerical dominance usually for two or less months in the year. This pattern was also found in the freshwater cladocerans, bivalve veligers, *Microcyclops* sp. and *Euterpina acutifrons*.

Fig. 10 Proportional representation of taxa comprising more than 5% of the total zooplankton abundance at site one.

Fig. 11 Proportional representation of taxa comprising more than 5% of the total zooplankton abundance at site two.

SITE ONE

Seasonal Abundance

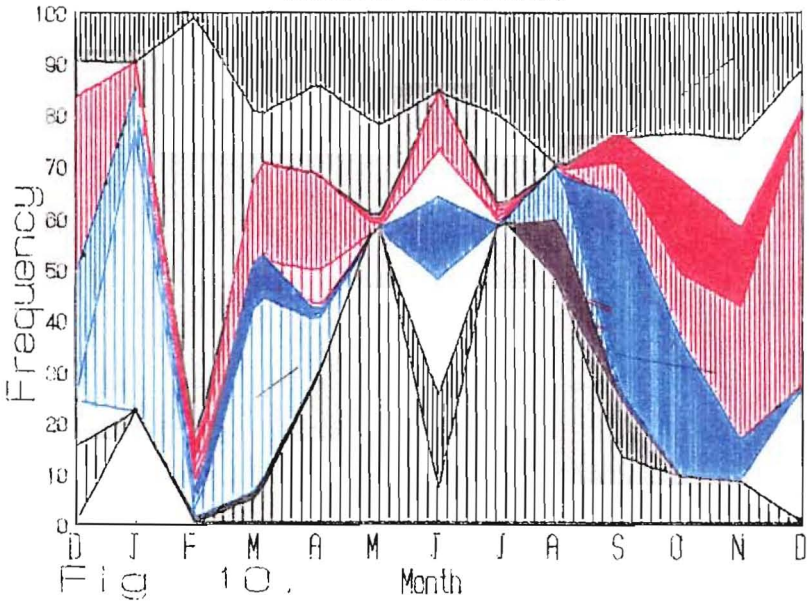


Fig 10.

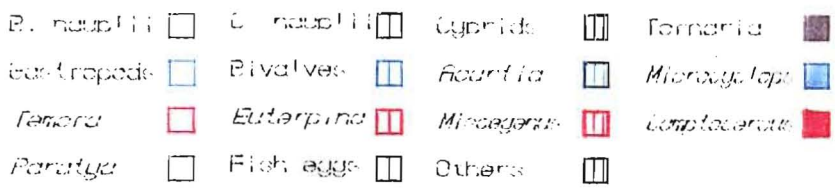
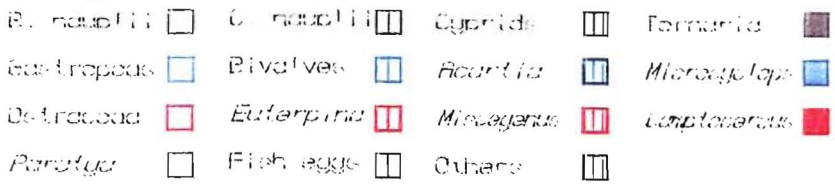
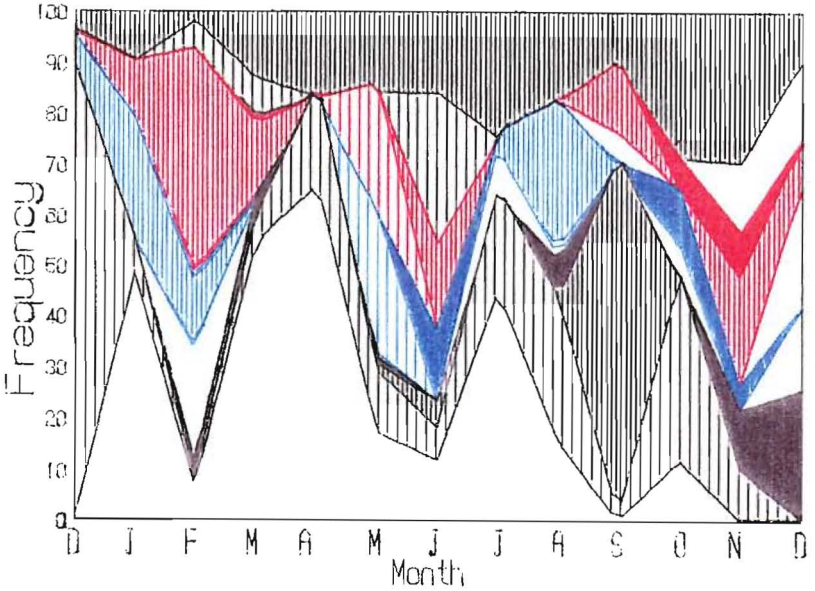


Fig 11.



SITE TWO

Seasonal Abundance



Two species of copepods, *Temora turbinata* and *Quinquelaophonte* sp. did not appear as major components of the zooplankton fauna at site two. Ostracods appeared very briefly as a new fraction of the dominant zooplankton taxa during September and December 1986.

Overall taxa abundances were much higher at site two than either sites one or three. This was mainly due to a few of the smaller species such as barnacle and copepod nauplii and tornaria larvae. These taxa reached abundances up to two orders of magnitude higher than those found at site one. High numbers of particular species affected the overall dominant species diversities by excluding those species which did not change in abundance. For example, although *Acartia* sp. were present throughout the year, increasing numbers of barnacle nauplii displaced their representation within the numerically dominant fauna during May and July (Fig.11).

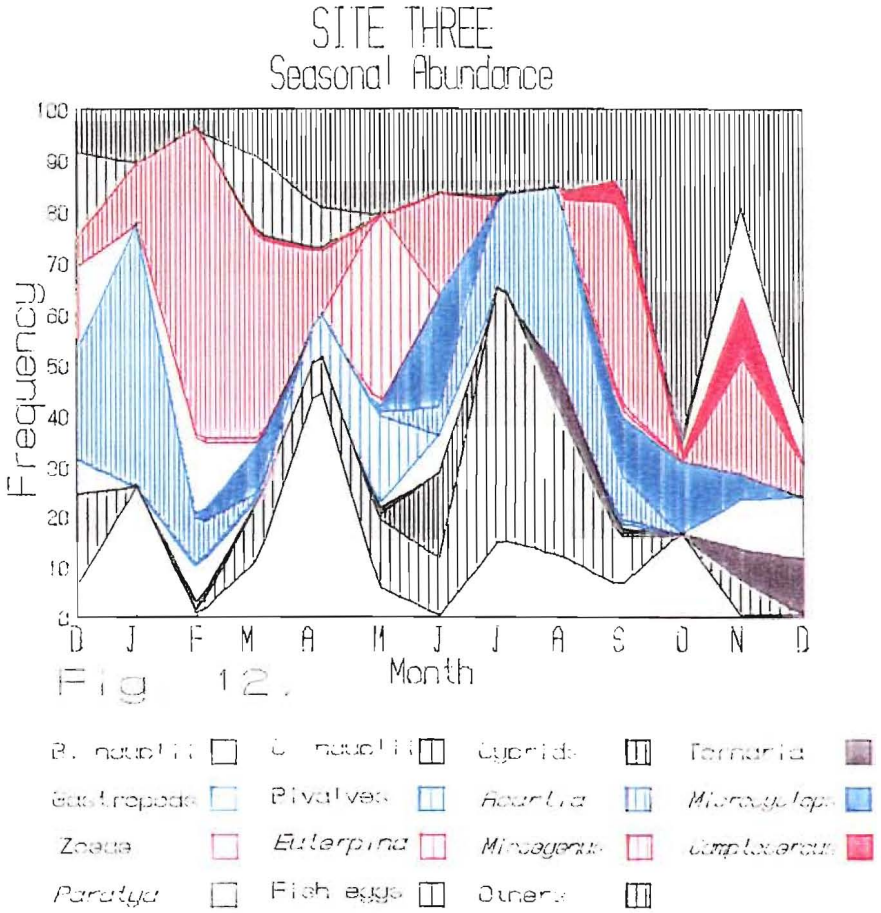
Site Three Abundances

Figure 9 shows that overall abundance of species at site three was reduced compared with site two. However, using the abundant taxa scale the number of major zooplankton taxa was increased by Brachyuran zoeae (Fig. 12). Otherwise proportions and dominance periods of species at site three were very similar to site two.

Seasonal Abundances

At all sites, species show three consistent patterns of occurrence. They are either present throughout the year, occur over a limited time period or occur irregularly. Continuous presence at site one was the dominant pattern exhibited by copepod nauplii. The same pattern was shown by barnacle nauplii at site two and by both copepod

Fig. 12 Proportional representation of taxa comprising more than 5% of the total zooplankton abundance at site three.


SITE THREE
Seasonal Abundance
Frequency
100
90
80
70
60
50
40
30
20
10
0
D J F M A M J J A S O N D
Month
Fig 12.
Cyprids
Ternaria
Bivalves
Acartia
Evterpina
Miracyclops
Zoaea
Microsetella
Paratya
Fish eggs
Others

and barnacle nauplii at site three. The seasonal occurrence of dominant species in sites two and three were similar with coastal and estuarine species equally represented.

Barnacle and copepod nauplii were species that remained members of the numerically dominant taxa through the year at both of sites two and three. At site one, copepod nauplii were present throughout the year except in December and January. At this time barnacle nauplii were dominant. After this period barnacle nauplii were no longer represented in the dominant zooplankton (Fig. 10). Copepod nauplii did not completely replace barnacle nauplii which were still present at site one. Copepod nauplii abundances have two major peaks of abundance at site one. The first occurred during May and the second in July. At these times, numbers of copepod nauplii reduced diversity of the dominant taxa to two species. During the intervening period decreased numbers of copepod nauplii allowed dominant taxa representation to rise to six. In June and September barnacle cyprid numbers increased, following rises in previous months of the barnacle nauplii abundances. Barnacle nauplii numbers were too small to be represented in the dominant fauna of May and July. Immediately following the rise in copepod nauplii abundance, increases in the combined copepod fauna took place.

Barnacle nauplii were the most numerically dominant taxa present at site two. Appearances of copepod nauplii were greatly reduced and tended to coincide with peaks of abundance at site one. However copepod nauplii were present in all the seasons to some extent as part of the dominant fauna. One difference in the distribution of copepod nauplii at site two was the appearance of a third peak of abundance during October. At site two barnacle nauplii exhibit four peaks of abundance occurring in January, March, July and October.

Site three had very similar abundance patterns of numerically dominant species to site two. The only major difference in abundance patterns was the reduced proportions of nauplii at site three compared with site two. This effect allowed diversity of dominant taxa to increase, and the proportional representation of the dominant taxa to increase.

Another pattern of abundance shown at site one is increased representation of species originating in freshwater during September through November to December. These increases in abundance lag slightly behind periods of high river flow. Typical representatives of this fauna are *Paratya curvirostris*, *Microcyclops* sp. and *Camptocercus* sp. Fish egg counts also exhibited a limited period of dominance at site one. They appeared in the numerically dominant fauna during January, increased markedly during February, followed by a continuous decline in abundance until September. This pattern of fish egg abundance was absent at sites two and three with other taxa contributing to the dominant taxa. For example ostracods and barnacle cyprids appeared during January through to August. Freshwater species exhibited increased abundances at sites two and three during September to December but were present in reduced proportions compared with site one.

The third pattern of abundance is those species continuously present during the year, but not represented in the numerically dominant taxa of figures 10,11 and 12. At the same time increased abundances of smaller taxa, such as the nauplii, decreased the relative representation of the less abundant taxa. The less abundant larger taxa include *Miscegenus heretunga*, *Acartia* sp. and Polychaete Tornaria. *M. heretunga* and *Acartia* sp. have been previously recorded as inhabiting estuaries and were intermittantly represented in the

dominant fauna. A reflection of this estuarine habit is apparent in their increased representation at sites two and three, both of which were situated within the estuary proper.

Cluster Analysis

Results of cluster analysis grouped species with similar abundances are shown in Figure 13 and sample sites and periods with similar total abundances in Figure 14. Because the abundance data is quantitative, these measurements have been used in the cluster analysis rather than constructing similarity matrices (appendices A-C). The information available within this data set reviewed spatial and seasonal species abundances.

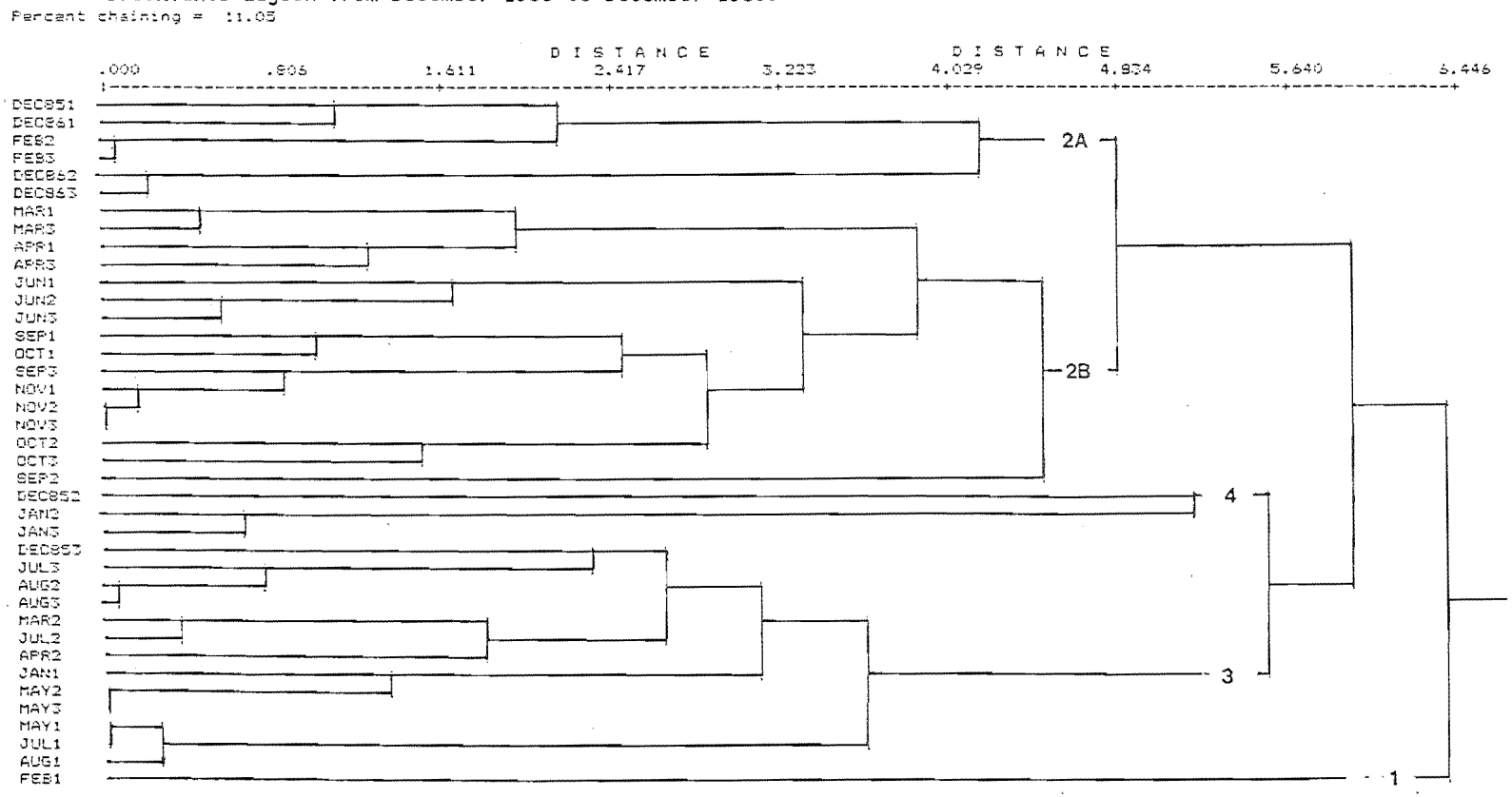
Site Clusters

Site clusters from seasonal samples have been arbitrarily selected at a relative distance of 5.237. This separation extracted four major clusters (Fig. 13). The first separation (group 1) was site 1 in February which separated alone at 6.40

All the remaining sites separated into two clusters of 16 and 22 sites at a distance of 5.94. The first major grouping (16) divided again at 5.54 and the second group (22) subdivided into two clusters at 4.834. Beyond this level the value of information extracted by statistical methods becomes ecologically indistinct.

Cluster analysis has grouped the summer months of December and February (group 2A, Fig. 13) and December and January (group 4, Fig. 14) together. Other months grouped by season are March and April for autumn and September, October and November corresponding to spring (group 2B, Fig. 13). Group three contains those seasonal samples with low zooplankton abundances and low diversities. These samples have been found at all three sites during May, July and

Fig. 13 Cluster analysis of numerical sample data from three sites in Brooklands Lagoon from December 1985 to December 1986.



August. Group three also includes all sites for December 1985, sites 3 and 2 in March and April and site 1 in January. Inclusion of a site 1 summer reading in this cluster offers no consistent seasonal pattern.

The second major group (22) is clustered into two sub-groups at a relative distance of 4.834. The first sub-group (cluster 2B) has a single outlier at site 2 during September. However the rest of this group (15 sites) gathers all the sites together from September, October, November, March (except site 2), April (except site 2) and June. These months are those with the largest number of floods and the highest average Waimakariri River flows (Prob. Chi-squared > 6.2308, df=2.5%). The second sub-group (cluster 2A) had six sites and contained a mix of summer abundances during December and February.

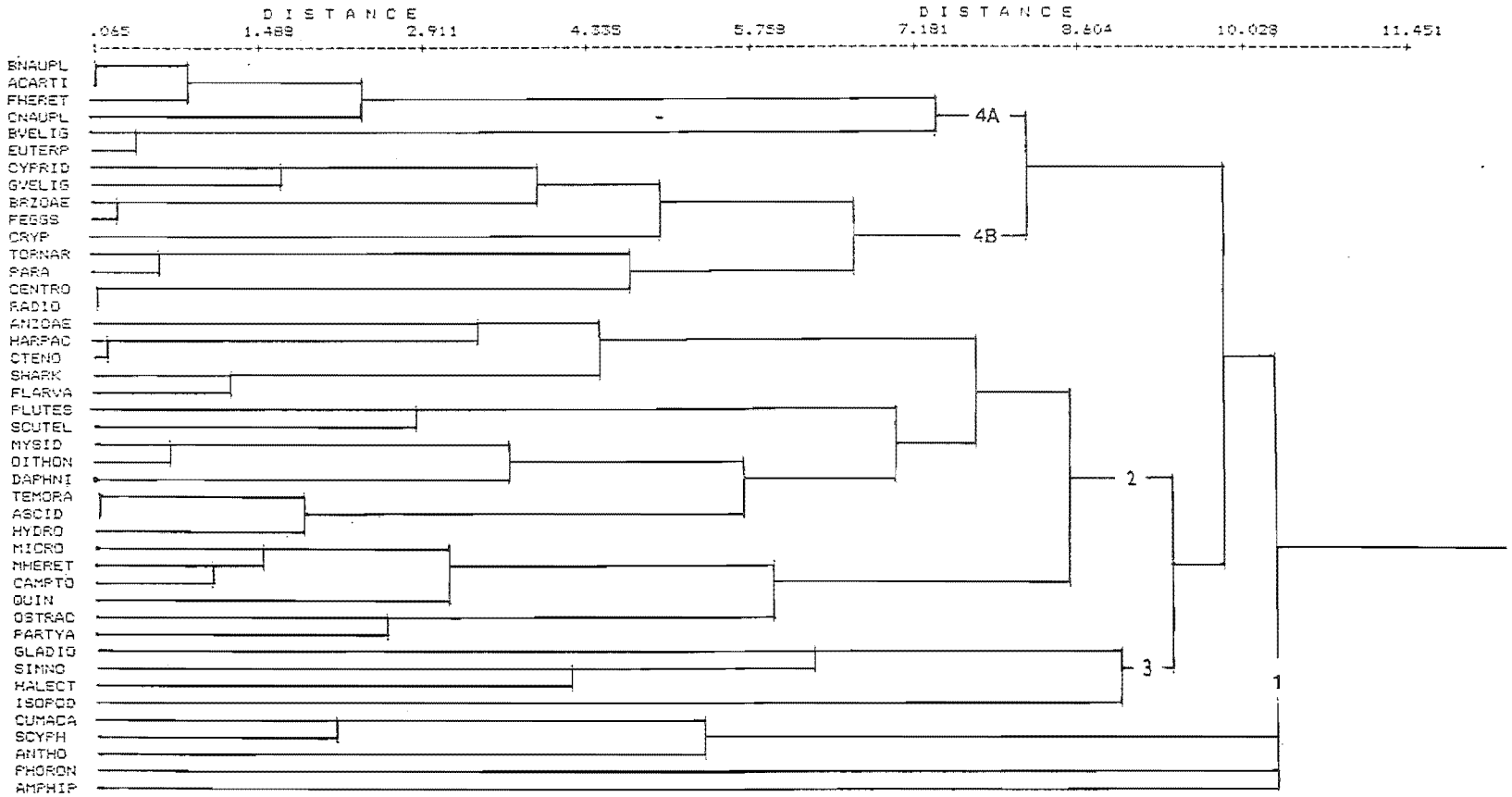
Species

The species clusters (Fig. 14) were produced on species abundance similarity between sites. These groups have been clustered according to environmental origins of the species. An arbitrary selection of clusters was made at a relative distance of 9.138 as cluster interpretation below this level became ecologically indistinct.

The first cluster (group 1, Fig. 14) of taxa separated at a relative distance of 10.295 and comprised the cumacea, scyphazoan coelenterates, polychaete larvae, phoronid larvae and amphipods. These taxa were all very rare in the samples and may represent a mixed group of outliers in the analysis.

The remaining species (36) subdivided at a distance of 9.950 into two groups of 21 and 15. These in turn also sub-divided. Descriptions of these groups use the labels shown in Figure 14. Group

Fig. 14 Cluster analysis of total fauna abundance from three sites in Brooklands Lagoon from December 1985 to December 1986.



three clustered at a distance of 9.405 with group 2 and included the rare copepod species *Gladioferans pectinatus*, *Simnocephalus vetullatus*, *Halectinosoma* sp. and an isopod. These species have all been recorded previously from the Canterbury region within an estuarine environment and are euryhaline (Bayly 1963).

Group 2 is a large cluster characterized by species from fresh and brackish water environments. These include, the mysid *Tenagomysis* sp., *Daphnia carinata*, *Microcyclops* sp., *Camptocercus* sp., and an Ostracod and *Paratya curvirostris*. A large proportion of the recorded harpacticoid copepods were also in this cluster. They were a sharknose harpacticoid, *Scutellidium* sp., *Miscegenus heretunga*, *Scutellidium* sp. and *Quinquelaophonte* sp. The harpacticoid copepods in Brooklands Lagoon are all euryhaline meiobenthic estuarine inhabitants (Hicks & Coull 1983, Wells et. al 1982) except *Euterpina acutifons*, which is a neritic species (Moreira et. al. 1982). Other taxa present in this cluster were: anomuran zoeae, Ctenophora, fish larvae, pluteus larvae, *Oithona similis*, *Temora longicornis*, Ascidacea and calypterous (hydro) medusae. These were all very rare but became abundant during summer. These species are normally recorded as inhabitants from marine habitats.

The second major group (group 4) split again at a relative distance of 8.159. None of the members of the final cluster are found in freshwater sources, except possibly the gastropod veligers which may be the undescribed veliger larvae of *Pomatopyrgus* sp. Nine of the fifteen taxa in this cluster are larval representatives of their taxa. Group 4A taxa are small but were very numerous and present for the whole year. They were the cirripede and copepod nauplii, bivalve veligers, *Acartia* sp.,and *Euterpina acutifrons*. Group 4B consisted of the larger copepods *Paracalanus indicus*, *Centropages aucklandicus* and

Barnacle cyprids, Fish eggs, Brachyuran zoeae, Cryptoniscid isopoda, Polycheate tornaria and Radiolaria. These taxa were generally present throughout the year, but not among the numerically dominant representatives because of the large numbers of the smaller (4A) representatives.

ORDINATION

Ordination was performed using similarity of species abundances for every collection site. This allowed the data to be separated spatially and seasonaly. This procedure produced three clusters roughly approximating those shown in earlier cluster analysis. This technique confirmed the earlier results of cluster analysis by plotting sites or species in groups, in ordination space, which could be circled in groups matching cluster results. Ordination produces a series of multidimensional correlations linking cause and effect of species abundance patterns to some extent.

Samples in Species Space

Data was ordinated as seperate samples enabling separation of seasonal and spatial distribution patterns. The resultant Bray-Curtis ordination axis one explains 75.66% of the variance and axis two accounts for 17.66% (Fig. 15). Total variance accounted for 93.32%. Extraction of more variance using further dimensions appears unjustified as the third and fourth axes account for only 4.21% and 1.20% of the variance respectively. Therefore, for the purposes of this study only the first and second extracted vectors will be used. Scatter plots have been made after the eigenvalues have been normalized by the transformation, ABS[log(x+1)]. Samples in each cluster have been labelled within groupings produced by earlier

cluster analysis, for visual interpretation. There are no scales are present on the axes of Figures 15 and 16 because they are hypothetical units produced by analysis.

Separation of the samples according to sampling sites one, two and three appeared randomly distributed in two dimensional ordination space. Separation of the data points by month produced no clearly distinct groupings. This was also the case for separate plots using broader seasonal grouping of raw site data and broader groupings of the monthly data.

Separating samples according to cluster analysis shows that the clusters can be separated in two dimensional space as clearly distinct groups. However environmental data have poor correlations with the axes produced. Salinity concentration shows the strongest relationship to the first axis (r=0.471). Temperature associates best with axis two (r=0.177), but this axis also has an equally strong association with Waimakariri River flood events (r=0.174).

Species in Sample Space

Bray-Curtis ordination of untransformed data of species abundance vectors in sample space explain 73.93%, 18.42%, 5.38% and 1.12% of the total data set variance in the first four axes. As the variance explained by axes three and four is less than 10% these will not be used in the final discussion. Axes one and two combined, explain 92.35% of the total variance. Species eigenvalues have been plotted on axes one and two using grouping described during cluster analysis (Fig. 16). For an easier visual interpretation vectors have been transformed using ABS[log(x+1)]. Because of the relative hypothetical units of these axes neither of the scales are labelled.

As a result species plots may be overlaid on the earlier samples ordination plot to highlight the most probable causes for each species abundance distributions.

Correlation of resultant eigenvalues with sample values shows that site two in January best describes the data for axis one (r=0.999) and site two in December 1985 best describes axis two abundances (r=0.999). However the groups are less distinct and have more overlap than the previous description of the data set by samples in species space and in fact this analysis accounts for less variance. Species overlayed on Figure 15 show that rarer species such as those in group 4 (Cumacea, Amphipoda and Scyphozoa) are present in ordination space representing low temperatures and low salinities. While more abundant species in group 1A (barnacle and copepod nauplii, *Acartia* sp. and *Euterpina acutifrons*) have plotted at higher temperatures and higher salinities, that is more distantly on the axes.

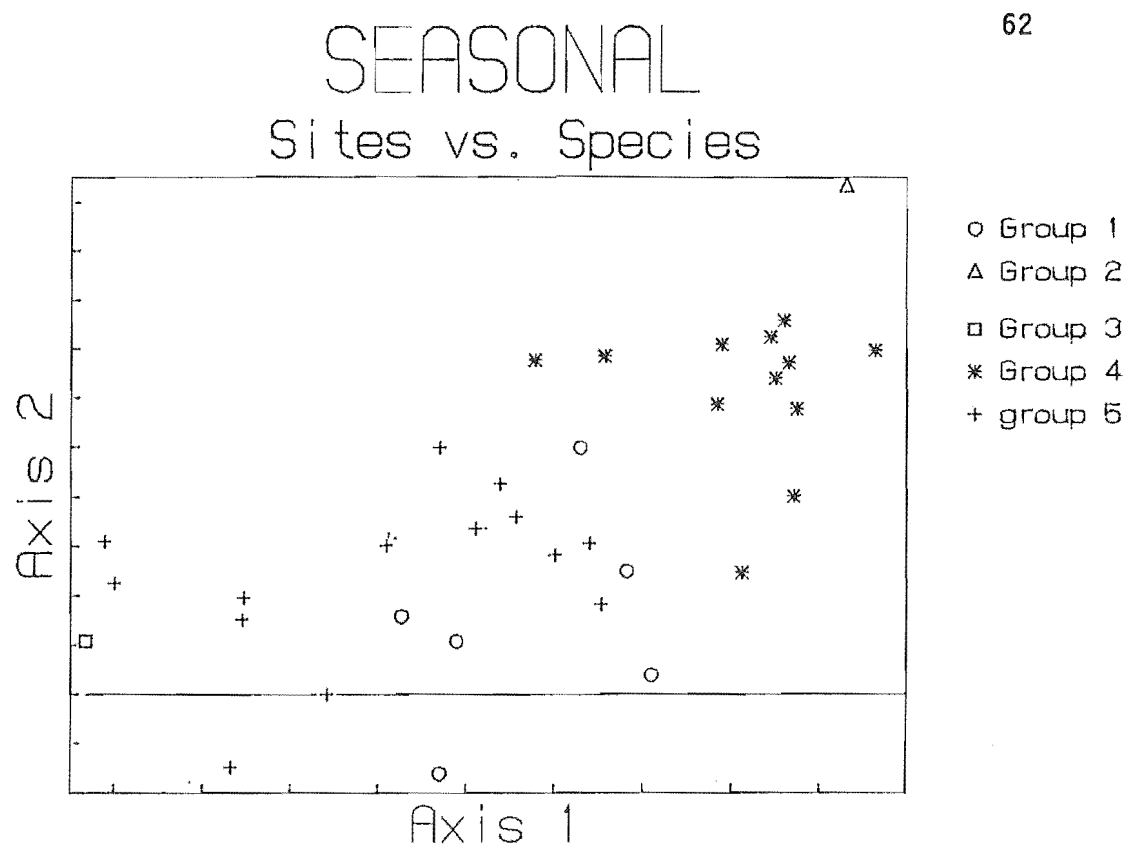


Fig. 15 Bray-Curtis ordination plot of total zooplankton abundance in for sample from monthly data from Brooklands Lagoon.

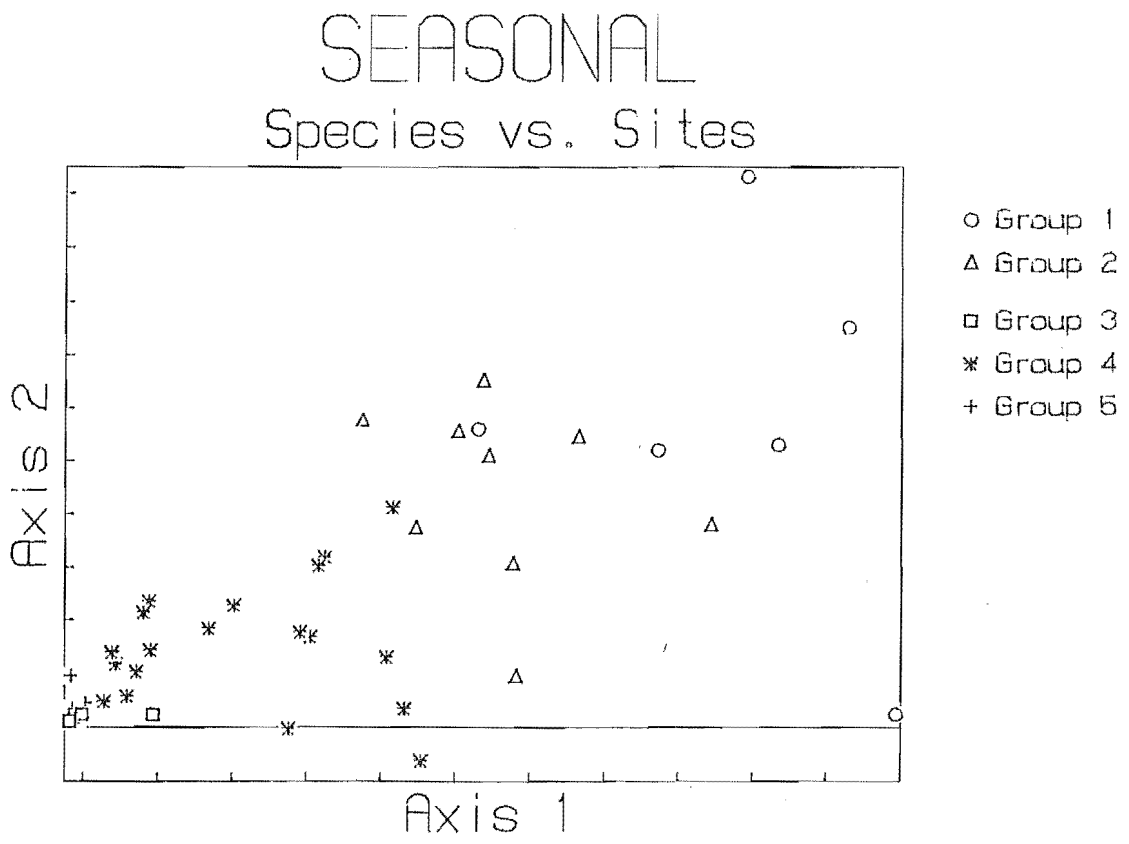


Fig. 16 Bray-Curtis ordination plot of species abundances from every sample from monthly data from Brooklands Lagoon.

DISCUSSION

ZOOPLANKTON DISTRIBUTION

PHYSICAL VARIATION

River flow is the most variable environmental aspect of the estuary hydrography. A seasonal pattern is evident with the highest flows occuring during spring, decreasing to an annual minimum during summer. No comparisons can be made with other studies as most record runoff into the estuary by measuring salinity dilution (Roper et. al 1983, Jeffries 1967, Deevey 1960a)

The annual cycle of temperature changes within Brooklands Lagoon is similar to many other studies in similar latitudes of the northern hemisphere. (Deevey 1960b, Jeffries 1967). For the same period of the year Roper et. al. (1982) showed virtually the same temperatures for the nearby Avon-Heathcote estuary.

Salinity has wide fluctuations within Brooklands Lagoon. Most other estuarine studies have shown salinities varying between 20-32 ppt in a regular linear fashion from the head of the estuary (Deevey 1960a, Jeffries 1967). The only close comparison can be made with the nearby Avon-Heathcote estuary (Roper et. al. 1983) where salinity may drop to 5ppt. The lower surface salinities found in Brooklands Lagoon demonstrate that the water is virtually freshwater (by definition 0-5 ppt).

Chlorophyll a concentration measures is not recorded in many zooplankton studies so comparisons can not be made.

Tidal changes appear to be influenced by the river flow in Brooklands Lagoon. When river flow is high salinity is correspondingly low indicating that the effect of the incoming tide is also reduced. This implies that sampling at high tide has not eliminated tidal variance from the study. Future research should build this variable into the seasonal sampling regime.

Relatively high oxygen tension (above 60% saturation) suggests that this factor does not limit zooplankton abundances. An effect may be present in conjunction with low river flow and low tide periods on warm sunny days. At these times benthic respiration is not buffered by a deeper water column of an incoming tide and the water in the lagoon is depleted in dissolved oxygen. This result compares favourably with Winterbourn et. al. (1971) who recorded saturation levels of 33% to 102% in the lower Waimakariri River after oxygen depleted water had been discharged from streams accepting wool scour and freezing works effluent. These factories have now been closed and the rapid reoxygenation demonstrated by Winterbourne et. al. shows that oxygen tension would never truly limit distribution for more than a few hours, if ever.

Patterns of Abundance

Total zooplankton abundances within Brooklands Lagoon describe patterns similar to those found by previous research in Chesapeake Bay and the Sargasso Sea and the North Atlantic (Deevey and Brooks 1971, Deevey 1960b, Jeffries 1967, Colebrook 1964). The summer maxima at each site occurred in January and this was approximately ten to fifteen times greater than the winter low abundances (cf. Hopkins 1977). Similarly increases in abundance were obvious during May and August, at the end of autumn and the beginning of spring. These occurred at the same time as peak chlorophyll a concentrations at sites one and two (cf. Deevey and Brooks 1971).

The general pattern of abundance highlighted by the seasonal zooplankton survey has shown that lowest abundances occurred at site one. A more expected pattern of abundance was established at the remaining two survey sites. Site two had the highest average abundances and site three had abundances an order of magnitude less.

Roper et. al (1983) found decreasing abundances of zooplankton progressing up the Avon-Heathcote estuary. Deevey (1960a) found that zooplankton within Delaware Bay were generally less abundant compared with simultaneous coastal samples. Evans and Grainger (1980) showed similar patterns of decreasing abundance toward the head of a Canadian arctic estuary. All of these sites had one important difference from Brooklands Lagoon. The freshwater inputs to these estuaries were at the head of the estuary and seawater was measurably diluted along the length of the estuary. In Brooklands Lagoon the main freshwater source, the Waimakariri River, flows past the mouth of the estuary, but seawater is still measurably diluted along the length of the estuary, if the estuary is not totally fresh.

Some zooplankton species have patterns of abundance in reverse of the general trends. Nearly all workers have found some species falling within this category. These species have been ascribed to the group of estuarine residentials or freshwater displacements (Roper et. al. 1983, Deevey 1960a, Evans and Grainger 1980, Jeffries 1962a). The same species, or at least the same families with different species representatives, are found within Brooklands Lagoon. In my study the estuarine resident species were an harpacticoid copepod, *Miscegenus heretunga*, Barnacle nauplii and Brachyuran zoeae.

Freshwater species can be safely excluded from the list of esturine residentials because they were more abundant at site one. This was due to the freshwater source flowing past the mouth of the estuary. In contrast to marine taxa, freshwater zooplankters in Brooklands Lagoon were the only species which had abundances declining uniformly along the length of the estuary. These taxa included *Microcyclops* sp., *Tenagomysis* sp., *Paratya curvirostris* and ostracods. *Microcyclops* sp. and *Paratya curvirostris* were both absent

from the survey of Roper at. al. (1983), but this may be a reflection of the biology of these two species. These species are both described as living normally in deeper lakes and faster flowing rivers respectively (Chapman and Lewis 1976). Both of these types of waters are absent from the headwaters of the Avon-Heathcote estuary.

At all the sites within Brooklands Lagoon meroplankton and other larval zooplankters comprise a small and transient proportion of the total zooplankton as described generally by Raymont (1983). Patterns of appearance of these groups are similar to those recorded by other researchers (see Raymont 1983 for review). Copepod nauplii show two peaks of abundance during the year in May and July. The first peak supports the theory that this life history stage is an over-wintering mechanism (Hopkins 1977, Jillett 1968). The second peak abundance supports the idea that copepod populations remain continuous breeders despite detrimental conditions. This makes them opportunistic in habit (Russell 1935, Bigelow 1926). If nauplii were an over-wintering stage only, there would be no second peak in their numbers during spring. Instead it could be expected that nauplii numbers would decrease and copepodite numbers steadily increase as the seasons became warmer.

Barnacle nauplii had four peak abundance periods during the seasonal survey at sites two and three. These are reduced in overall proportion at site three and almost non-existent at site one. This is a different pattern to that described by Raymont (1983) who said that nauplii abundances peak only during spring. However Raymont also suggested that this group was continually reproducing. Because the group was not identified to species level it cannot be determined if the abundance peaks shown by this group represent a single species or fluctuations in abundance of several species.

Polycheate tornaria larvae had peak abundances in spring and early summer as described by Raymont. Fish eggs also fit the standard seasonal pattern of peak abundance during summer described by Raymont.

Fluctuation Causes

Poor correlation with environmental data can be expected for the ordination data set, as several of the variables in this case affect each other in a feed-back response. For instance, temperature affects rainfall and then river flow. Low correlation does not mean that the measured variable is having little effect within the estuary system. Poor correlation may indicate that not enough data have been collected to give a better indication or that the variable is a co-associate with another. In the case of axis two, in the samples ordination, temperature and flood events may be acting simultaneously to affect the zooplankton abundance. Positive correlation with salinity and temperature plus flood events indicates low values for sites plotted close to the origin of Figure 16.

Site one in February formed a group on its own. This site was characterized by a high river flow due to high country rain the previous week and a simultaneous spring tide component, but February had fewer floods. Both of these environmental parameters have allowed a large overall zooplankton abundance due to marine and freshwater inputs to the lagoon. Warm temperatures at this time of the year resulted in a large chlorophyll a concentrations which were the most likely food source of the zooplankton in the estuary (Fig 8).

The groups 2A and 2B (Fig. 15) produced by cluster analysis comprise those periods and sites during the year with high average river flows. These sites and seasons occurred mainly in spring and late summer. Group 2B actually appears below the third level of

similarity and is really only a sub-cluster of the group 2A. However this cluster comprises two-thirds of all the December readings. December was a period during 1986 and 1985 when water temperature was highest and tidal flushing was greater within the lagoon.

These seasonal patterns of sample clusters explained in the results all have similar river flow patterns. Flow patterns broadly evident from Figure 4 show peak flows in late winter and early spring, that is August and September. Lowest flows are shown in the summer months December and January. Low river flow is also a feature of the autumn period March and April, while February is a month of unusually high summer river flow. Confirmation of this interpretation is provided by Bray-Curtis ordination.

Ordination shows that all clusters apart from 2A and 2B (Fig. 15) are separated by the first two axes. Correlation of environmental variables with axis one showed salinity was the best descriptor of the variance in this axis which may be interpreted as an indirect measure of the tidal force. This implies that the degree of saltwater mixing within the estuary is the most important variable affecting distributions of zooplankton within Brooklands Lagoon. On axis one alone, which describes 75.66% of the data set variance, all of the clusters can be partially separated. Because salinity is a variable highly influenced by mixing of coastal and freshwater sources within an estuary it could be argued that the largest of these two forces is the ultimate determination process for hydrological conditions within the estuary. Hydrological conditions in turn determine the distribution of the zooplankton by definition (Raymont 1983, Bougis 1976). As the Waimakariri river had very large flows during most of my study, river flow could be the most important determinant of zooplankton presence, from either marine or freshwater sources in Brooklands Lagoon.

Axis two of the ordination correlates best with temperature and flood events. As zooplankton are notable opportunists (Raymont 1983) they could be expected to be limited in this environment by unfavourable conditions such as freshwater flow (limiting distribution Bayly 1963) and low temperatures (slowing metabolism and breeding, Davis 1984, Conover 1960). Axis two, although less discriminatory 17.64% of data set variance explained than axis one, spreads that ordinated points into two dimensional space and graphically clarifies the clusters. Most clustered groups appear to cover a wide range of temperature and lower frequency of floods. This can be expected for the more widely distributed species which all have wide temperature tolerances, and are usually euryhaline (Van der Spoel & Heyman 1983). This effect can be seen as overlap of cluster groups along axis two. When overlayed on the samples plot species plots mostly fall close to the origins of the ordination. This represents environmental conditions of less frequent flooding, lower temperatures and lower salinities. The depressed temperature and salinities associated with these species distributions are unusual (Van der Spoel and Heyman 1983). This fact supports the theory that these variables are secondary in importance to the frequency of flood events within Brooklands Lagoon. Further readings over continuing seasons would clarify this picture giving each cluster of points a tighter definition (Gauch 1984) by including more points in each group.

The rarest species (group 1, Fig. 16) such as the Cumacea, Scyphozoan jellyfish, phoronid larvae and amphipods are seen to be least tolerant of frequent freshwater disturbance, or better able to remove themselves from its effects, because these groups are in a postion of the ordination plot showing preferred lower salinities and low temperature distributions. At higher temperature and

salinity distribution position within the ordination (and consequently greater flood disturbance) are found the clustered species with the next highest abundances. This group (group 3, Fig. 16) consisting of *Gladioferans pectinatus*, *Simocephalus* sp., *Halectinosoma* sp. and the Isopoda. Group 3 were present in larger abundances with similar patterns of environmental distribution for groups 2, 4B and 4A with increasing abundances respectively, reaching up to the right hand corner of figure 16.

Sites and seasons corresponding to the first cluster groups, that is those with highest salinity and temperature, generally occur when tides are highest and river flow is lowest. Because river flow is lower during these periods the implication is that the weather of the previous week has been relatively fine and fair weather offers a maximum of sunlight for phytoplankton production of chlorphyll a. This effect follows through the estuarine food web from the phytoplankton to the zooplankton.

Furthermore those benthic species within the estuary that release planktonic larval stages are also able to grow and reproduce during these favourable conditions. The offspring of these species swell plankton numbers dramatically for short periods (Raymont 1983). The overall effect of fair weather then, is an increase in the numbers of estuary-derived zooplankton. High production rates of meroplankton within the estuary tend to overshadow less abundant larger species. This means that holoplankters such as *Paracalanus indicus* and *Centropages aucklandicus* which appear as members of cluster 1B, are in fact relatively more abundant and are grouped with the meroplankton.

Another inference from this analysis might be that rare species are those displaced by competition for food (chlorophyll a, the most likely food source for the mainly herbivorous taxa found in this

study) into less desirable habitats such as estuaries. These habitats would be those of lower salinities and less protected from floods, in either space or time. Another alternative may be that the rare species are stenotaxic, estuarine species, only entering the zooplankton from shelter in the benthos during periods of favourable conditions. As a consequence they may be less abundant due to infrequently occurring fair weather periods for chlorophyll a production . Marine phytoplankton species would be sparse due to reduced salinities, or strong seaward surface flow from the river mouth while freshwater species of phytoplankton would be killed by increasing salinities as they are washed downstream.

CONCLUSIONS

Although long term studies of the seasonal abundance of zooplankton are rare, they all demonstrate major changes from year to year in the life cycles and breeding patterns of many species (Colebrook 1964, Deevey 1960a). In general many of the species in a single order have an average peak abundance during a particular season though (Raymont 1983).

Overall the holoplankton is composed of many species. However this group is mainly represented by the Copepoda and although they represent a single taxon each species has a slightly different life history. *Acartia* sp. and *Paracalanus* sp. generally show minimum densities in autumn. *Temora turbinata* has peak densities in mid-summer (Raymont 1983). Cyclopoid copepods and harpacticoid copepods usually show sporadic bursts of breeding throughout the year (Reeve 1963). *Oithona* nauplii peak in autumn and *Acartia* nauplii peak in spring. These patterns of abundance have all been clearly shown in

the present study. Sesaonal peaks of total abundance were not different from those described in other studies (Colebrook 1964, Deevey 1960, Deevey and Brooks 1971, Jeffries 1967).

Complexed with the timing of life histories is another factor of generation length. Given optimum conditions some species are able to reproduce as quickly as *Pseudocalanus parvus* in 3-4 weeks (Davis 1984). Many species of zooplankton are opportunistic, able to take advantage of any environmental change in their favour, such as unseasonal phytoplankton production, to reproduce. This factor has been demonstrated by increases following periods of decreased river flow and warmer temperatures, allowing phytoplankton populations to increase.

Generally holoplankton species show peak abundances during the warmer months of summer and autumn. Decreased numbers of adults are replaced during winter by larval stages such as copepod nauplii. This factor shows the importance of the larvae as an over wintering stage (Hopkins 1977, Deevey 1960b). Rich lipid reserves of copepodites tends to suggest that this life history stage is an overwintering stage also (Jillett 1968). However the continual appearance of nauplii and copepodites during the winter in this study suggests that populations are still breeding (Russell 1935, Bigelow 1926).

Seasonal patterns of abundance for the sub-antarctic waters may be pertinant to the fauna of the Canterbury coast. Weather patterns can force water masses from the sub-antarctic up the east coast of New Zealand. (Heath 1985). These currents would carry species northward, to complete their life history in New Zealand coastal waters (Bary 1959). *Calanus* sp. from the sub-antarctic region have peak abundances during spring and early summer. This population produces many copopedites which are carried to warmer waters for

over-wintering (Jillett 1968). Hardy and Gunther (1935) found the greatest seasonal variation in zooplankton populations of Southern ocean waters in the top 50 meters. This is the same level as the dominant coastal currents defined by Heath (1985).

In Arctic estuaries large melt flows and abrupt freezing at the start of the winter make reproductive timing crucial. Benthic species in these climates exhibit life histories of compressed reproductive stages where gametes and larvae are released in short, concentrated bursts during the brief summer months of May and June. It is thought that many Antarctic species avoided this problem by omitting planktonic larval stages from their life histories. Very few studies have collected meroplanktonic larvae in the Antarctic regions (Pearse 1969). However this study periodically found large numbers of meroplankton suggesting that colder temperatures associated with southern currents are not regular enough to affect coastal marine species as far north as the Canterbury coast.

River flow (measured in cubic meters per second) is probably the single most important factor affecting the zooplankton abundance within Brooklands Lagoon estuary. When river flow is low the tidal compartment is the primary hydrographical influence. This hypothesis however needs verification by surveying to eliminate variance due to day period and tidal cycle so that only river flow is tested. As it stands the evidence is circumstantial. This is because it ascribes cause to secondary parameters rather than those that are the primary result of the statistical analysis, namely salinity, temperature and frequency of flood events.

Given that river flow and tidal cycles are the primary hydrographical variables in the estuary affecting zooplankton abundance, it can be seen from analysis that from time to time other variables come into effect. In warm weather during the summer which

is when river flow is lowest, chlorophyll a concentrations may increase rapidly. This would allow the opportunistic zooplankton to take advantage of the favourable conditions for breeding. Also when river flow is decreased distance form the sea of each of the sampling stations may also affect distributions.

Some species abundances that were always quite high can obviously be used as indicators of environmental conditions. For example barnacle nauplii indicate the spread of residential or retained estuarine waters (r=0.990) and so to do *Acartia* sp. (r=0.918). *Centropages aucklandicus*, a neretic copepod would be a good indicator of seawater flushing the estuary (r=0.922).

I propose that estuarine systems at the mouth of large volume alpine rivers are limited by that rivers flow. That is that the river flow acts as a valve to the estuary system. Large flows prohibit coastal energy inputs to the estuary system which increase as river flow decreases.

CHAPTER THREE

ZOOPLANKTON DIEL SURVEY

INTRODUCTION

Many surveys have noted that zooplankton show diel migrations, usually moving toward the surface during periods of darkness and downwards during periods of daylight (Russell

1931, Sewell 1948, Hardy and Gunther 1935). Many reasons have been proposed for this behaviour.

The simplest theory for diel migration is that the zooplankton are maintaining a preferred light regime (Ewald 1912). Zooplankton cannot tolerate too much light, but need some. In more intensive daylight conditions they move deeper. Migration towards the surface occurs when light is diminished during darkness or moonlight conditions.

Another commonly accepted theory is that the zooplankton are moving away from predation pressure during daylight (Vinogradov 1970). At this time the zooplankton are more visible in silhouette to planktivorous fish larvae which hunt using visual cues. At night the zooplankton move back to the surface to feed when they are less obvious to visual hunters.

A third theory contests that the zooplankton do not migrate down from the surface during daylight, but disperse more evenly to greater depths in search of optimal phytoplankton concentrations (Hardy 1956). During daylight, light penetrates the water column further. Deeper light penetration allows greater primary production and hence herbivorous zooplankton are found to greater depths in the daytime, over phytoplankton concentrations are too high for efficient feeding, reducing the competitive success of zooplankton.

A second theory proposed by Hardy (1935) is that the regular movement between surface and deeper layers allows zooplankton to be carried further at night by passively drifting. Hardy pointed out that the currents at different depths are often moving in different directions and at greater speed than at the surface and distribution of a species would be greater if all currents were used.

Diel migration of zooplankton in estuaries has been recorded as the appearance and disappearance of fauna with each tidal cycle (McLusky 1981). Within estuaries zooplankton records show that the most abundant fauna are usually meiofauna. This group includes many harpacticoid copepods, isopods and amphipods which become planktonic in existence for part of each tidal cycle (Coull 1979, Coull & Wells 1981; Hicks & Coull 1983, Deevey 1960a). Many of these species depend on substrate particle size and salinity within the benthos to shelter during low tide. An important aspect of this existence is that these species may shelter from extreme conditions such as floods, which depress salinity and flush the estuary contents out to sea. However, this behaviour is complicated by the tidal patterns. Animals may be forced to emerge during daylight high tides while the tidal pattern is not synchronised with the photoperiod. Furthermore animals may be forced to shelter in the benthos for extended periods while contributing rivers are in flood, least they be swept into the sea. Zooplankton may break normal diel patterns of periodicity to feed after forced periods of starvation.

Within estuaries regular short term migrations may allow some species to maintain their locality. Bosch and Taylor (1973) showed the cladoceran *Podon polyphemoides* had a reversed migration pattern wi Chesapeake Bay. Sandifer (1975) showed that several *Cancer* species zoeae used this strategy in a variety of locations to maintain their estuarine habit.

A survey of periodic diel zooplankton abundances was undertaken in Brooklands Lagoon during February 1987. This was the predicted time when zooplankton concentrations would be highest (Chapter 3). The aim of this section of work was to establish if any of the estuarine zooplankton species showed diel periodicities and to discover any possible environmental factors that animals may be responding to.

METHODS

Field Sampling

During February a diel zooplankton survey was made at site two. This site was chosen because it had the greatest total taxa diversity and the highest abundances of zooplankton during the seasonal survey. Site two also had water present at all times to float the boat.

In general the same methods were used in the diel survey as in the species diversity survey, however an Horiba metre was used to measure dissolved oxygen, conductivity, temperature and water turbidity. Site two was sampled every three hours approximately, during periods of high, low and mid tide levels, for thirty hours. During each sampling period five repeated trawls were made and later subsampled three times to obtain average taxa counts. The thirty hour duration enabled two tidal cycles to be sampled; however only a single period of darkness was encompassed by this time, due to longer daylight periods in the summer.

The same physical and chemical variables measured during the seasonal survey at site two were measured during the diel survey. These measurements were also used for correlation purposes during the statistical analysis of zooplankton abundance.

The resulting taxa abundance data were averaged to obtain species densities for each sample period. This data was then used for cluster analysis and Bray-Curtis ordinations and correlations. Ordination was performed using similarity of taxa abundances during sample periods. Groups of points in two-dimensional space produced by Bray-Curtis ordination roughly approximate those found by cluster analysis. Data were normalized by logarithmic transformation of abundances.

RESULTS

DIEL SURVEY

Physical and Chemical Parameters

The findings of this part of my survey are shown in Figure 17. Tidal height and a bar showing the photoperiod have been added, as other factors have varied simultaneously with the diel light cycle and the tide.

The temperatures shown in Figure 17 were relatively high compared with average seasonal values obtained earlier. A significant drop in temperature occurred during the hours of darkness, with a rise again to a daytime peak during the next day.

Salinity (Fig. 17) showed uniformly low concentrations. This illustrates the dilution effect occuring within the length of the estuary, due to the Waimakariri River flow.

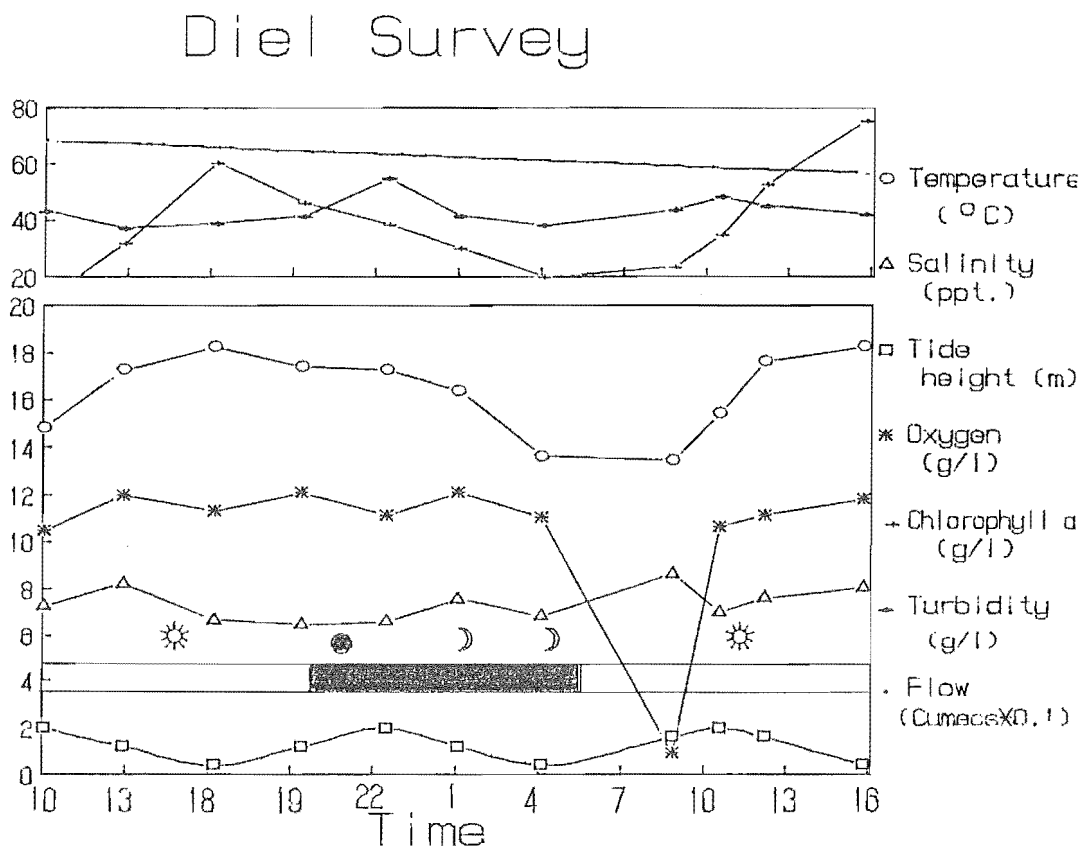


Fig. 17 Measures of physico-chemical variables and chlorophyll a concentration during diel zooplankton survey in Brooklands Lagoon, 19 February 1986.

The tidal periodicity was quite regular during the diel survey (Fig. 17). Previous records for the Canterbury region (Naval Hydrography Records) show days of a single tide for Lyttelton and the Canterbury coast, but these were not evident during my survey.

Figure 17 shows that chlorophyll a concentration changed markedly with a regular rise and fall corresponding with the hours of daylight and darkness. These readings were high in the late afternoon (4:00 pm) and low in the early morning (4:00 am). This regularity appears to be independant of the tidal periodicity. The tide has a period corresponding to the lunar period while the chlorophyll a production is in synchrony with the solar period.

Turbidity tended to rise and fall regularly during the survey in exact measure with the tidal period. This is most likely due to floculation of suspended particles due to changing pH at the freshwater:saline interface (McLusky 1981).

Oxygen concentration (Fig. 17) showed relatively constant levels during daylight, but a sudden decrease during early morning. This was associated with a decrease in phytoplankton biomass (represented by chlorophyll a concentration) during the night. Simultaneously there was an increase in total zooplankton abundance as the tide filled the estuary.

Taxa Diversity

Table 6 shows the abundance of taxa collected during each trawl. During the diel of this survey 35 taxa were counted and identified to species level where possible.

The number of taxa ranged from 19 to 27 (Fig. 18). Lowest diversity occurred in the two samples collected during afternoon low tide periods, at 4:15 pm. The highest number of taxa (27) occurred

TABLE 6. Number of taxa counted from samples corresponding to tidal component and photoperiod.

	TIDAL COMPONENT				PHOTOPERIOD	
	HIGH	LOW	MID IN	MID OUT	LIGHT	DARK.
	28.0	19.0	28.0	3.0	23.3	24.0
	24.0	26.0	27.0	2.0	25.0	27.5
	27.0	26.0	-	0.0	-	-
Average	26.3	23.7	27.5	1.7	24.2	25.4

twice, coinciding with incoming tides during the morning and the early evening of the first day. High values of taxa tended to occur with the high tide periods (Table 6).

A sharp decline in the average number of taxa found occurred on the receeding tides. The most notable absence during these periods were ascidean larvae, Ctenophora,coastal representatives and *Daphnia carinata* and *Simocephalus vetulus*, freshwater species. During the receeding tides salinity was higher and lagged behind the measured high tide (Fig. 17). Fluctuating salinity values suggest that a great deal of water mass mixing occurs within the estuary, to dilute the seawater.

Taxa periodicity was an obvious feature of the thirty hour survey. Three distinct fluctuations of similar amplitude were apparent. However these had irregular periods. The fluctuations were not significantly associated with changes in the photoperiod. Associated with changes in the photoperiod were obvious differences in the types of taxa present. Those taxa present only during the hours of darkness included barnacle cyprids, the freshwater mysid *Tenagomysis novaezeelandiae* and the cladoceran *Camptocercus* sp. Taxa which were present only during the day included the Ctenophora, cryptoniscid isopods, and the harpacticoid copepod *Halectinosoma* sp.

Taxa Abundance

Total zooplankton abundance in Brooklands Lagoon is shown in Figure 19. Both, total zooplankton abundances and taxa diversity show obvious changes over time with total abundances showing greater changes than taxa diversity. During daylight, numbers and diversity gradually decreased until late afternoon when the tide was ebbing. This was followed by a steep rise in numbers and diversity during the early evening on a flood tide during a period of total darkness before the moon rose. After the moon rose at 22:00 hours, numbers dropped sharply with a corresponding ebb tide period to the same level of abundance as the earlier daytime high tide. Total zooplankton abundance decreased again with the early morning flood tide, but diversity rose. During this time phytoplankton chlorophyll a concentrations were very low. As the sun rose total abundance and taxa diversity dropped with the flood tide, following a short period of lower dissolved oxygen concentrations (Fig. 17). Abundances started to rise during the final low tide period, but chlorophyll a concentration and dissolved oxygen concentrations were also high.

The relative proportions of zooplankton in Brooklands lagoon during the thirty hour diel survey is presented in Figure 18. Only species with abundances representing more than 5% of the total zooplankton count during each sample period are shown.

Abundances of the most numerically dominant species extend through several time periods. Only gastropod veligers, which would normally be expected to be present in high numbers during February, were numerically dominant throughout the diel survey.

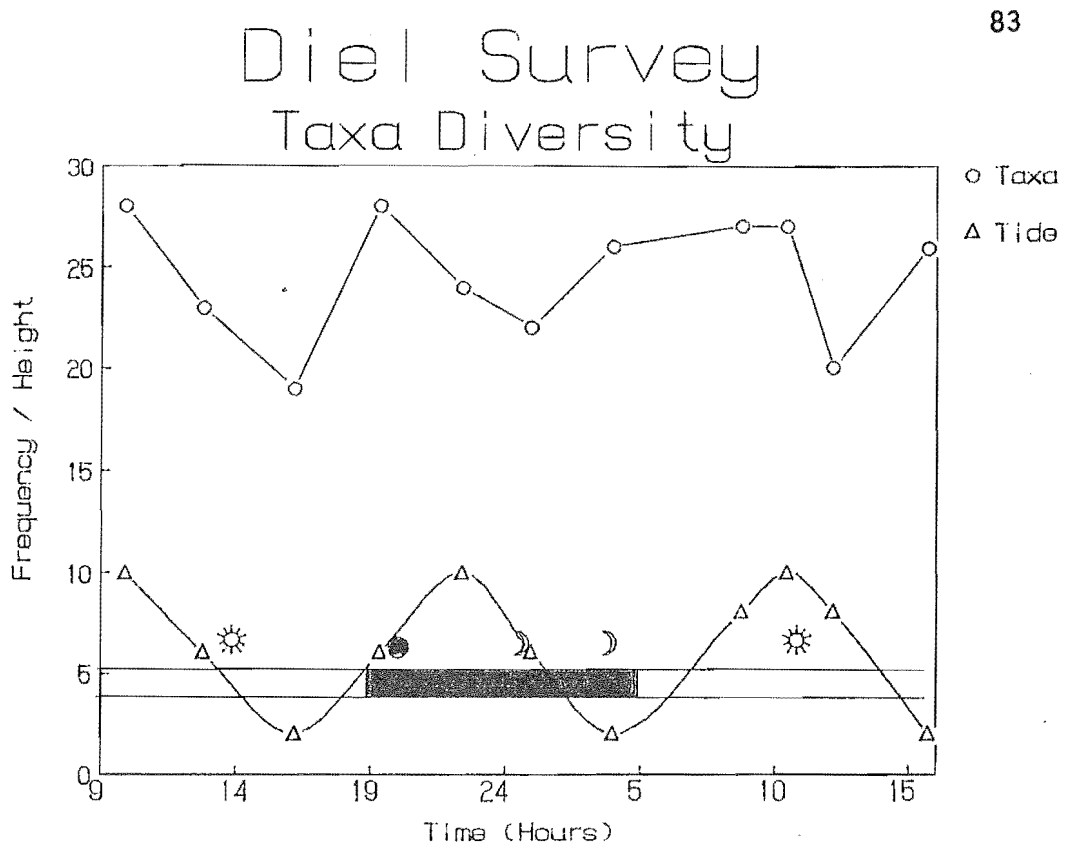


Fig. 18 Total zooplankton abundance for 30 hours in Brooklands Lagoon during diel survey.

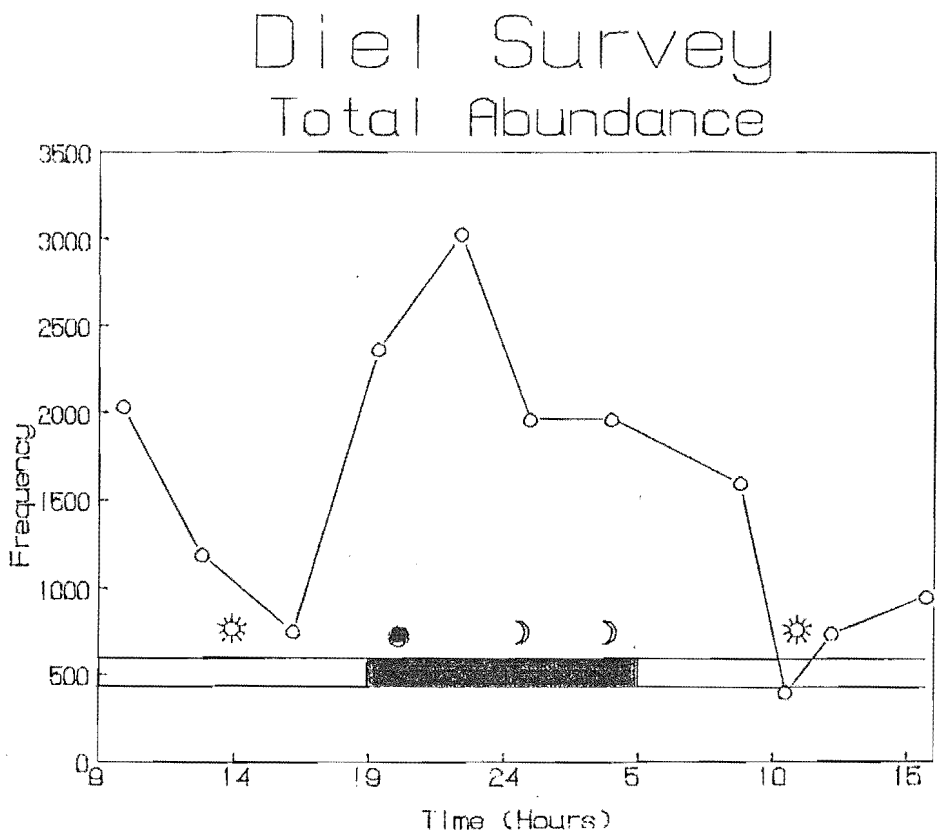


Fig. 19 Total plankton taxa diversity and tidal period in Brooklands Lagoon during diel survey.

Other species also showed distinct increases in numbers corresponding with obvious changes in the physical environment. For example, tornaria larvae were numerically dominant in samples for three short, but separate periods. These times corresponded with the out flowing tide and were even more accentuated during the time of complete darkness, 10:30pm.

Abundances of fish eggs showed a dramatic increase during the early hours of darkness. Fish eggs were found in all samples except those taken during the early morning of the first day. This phenomenon seemed to be independant of the state of the tide. Abundances of fish eggs gradually decreased through the night from an early evening peak of approximately 2082/l. At sunrise fish eggs had distinctly decreased relative to their dominance in the total zooplankton abundance. During the early morning ebb tide, fish eggs were no longer part of the dominant taxa.

Morning samples all showed greater abundances of meroplankton. Most abundant in this sub-group were the barnacle nauplii, closely followed by copepod nauplii. During midmorning greater numbers of herbivorous holoplankters appeared. The first and most abundant species to occur were the copepods *Euterpina acutifrons* and *Acartia* spp. As overall diversity increased the numerical dominance of the earlier taxa was depressed. Only gastropod veligers and barnacle nauplii remained members of the dominant zooplankton during midmorning.

During the midday low tide regime dominant holoplankters were represented by freshwater taxa including ostracods and *Daphnia carinata*. Although the types of taxa comprising the dominant groups had completely changed, meroplankton again became the dominant type of zooplankton. At midday these included barnacle nauplii, brachyuran

zoeae, gastropod veligers, polychaete tornaria, fish eggs and fish larvae. At this time dominant holoplankton were replaced by freshwater species, for example *Paratya curvirostris* and Ostracoda.

Brachyuran zoeae numbers were greater during midday low tides where they comprised 12 percent of the dominant zooplankters. This group was absent during coinciding periods of darkness and low tide.

After sunset and before the moon rose, during a period of total darkness, there were 24 recorded zooplankton taxa. However only two taxa were in numbers great enough to be included as dominant fauna. These were fish eggs and *Euterpina acutifrons* (an harpacticoid copepod) both of which were absent during midday and later evening samples.

As the moon rose and the light intensity increased so did the diversity of the dominant fauna. In the moonlight there were six dominant taxa present with roughly equal proportions of numbers. Freshwater holoplankton taxa were apparent in this assemblage taken during low tide. These species were *Paratya curvirostris*, *Daphnia carinata* and *Microcyclops* sp.

One noticable change in taxa abundance during the dawn was the replacement of *Daphnia carinata* by *Paratya curvirostris* as the dominant freshwater holoplankter. This decapod is larger and a more active swimmer than *Daphnia carinata*. Dominant taxa were replaced by more actively swimming daylight forms during the post-dawn sample. These taxa included brachyuran zoeae, gastropod veligers and *Paratya curvirostris*.

Some species were apparently only present during specific stages of the tidal cycle. For example numbers of the calanoid copepod *Acartia* sp. were only significantly dominant during half phases of the tide, that is during ebb and flow conditions.

Cluster Analysis

Results of cluster analysis using similarity of species abundance for data separated into eleven periods during the survey are presented. These covered a range of daylight, darkness and four tidal conditions.

Sample Times

Samples from each three hourly period were clustered as shown in the dendrogram of Figure 20. Four main clusters were produced. The first cluster consisted of samples E and F taken during full moon periods on a full or ebbing tide. These two samples appear to be almost totally similar with an average species diversity of 24 and 22 taxa respectively. All taxa during periods of full moon had high abundances, but extreme numbers of fish eggs separated these two periods from all others.

The remaining clusters divided again at a relative distance of 0.878. Period A (9:55am) formed a cluster on its own. This was the only daylight full tide sample and only had a few numerically dominant species. Low river flows and a high tide may have caused very good water column mixing to produce an overall high taxa diversity (27). These conditions would have mixed species from a variety of sources including freshwater, estuarine residents and coastal zooplankters.

The remaining eight sample periods split into two clusters of 5 and 3. The third cluster is the largest in this dendrogram and contains periods B, H, D, G and K. These were taken at times throughout the day, 12:55pm, 8:45am, 7:20pm, 4:00am and 3:45pm. There were no full tide observations in this cluster of times. All of the third cluster samples were taken on incoming (H & D), or low (G & K) or ebbing tides (B). All of these periods had high diversities

g. 20 Proportional representation of taxa comprising more than 5% of total abundance at site two, Brooklands Lagoon, during diel survey.

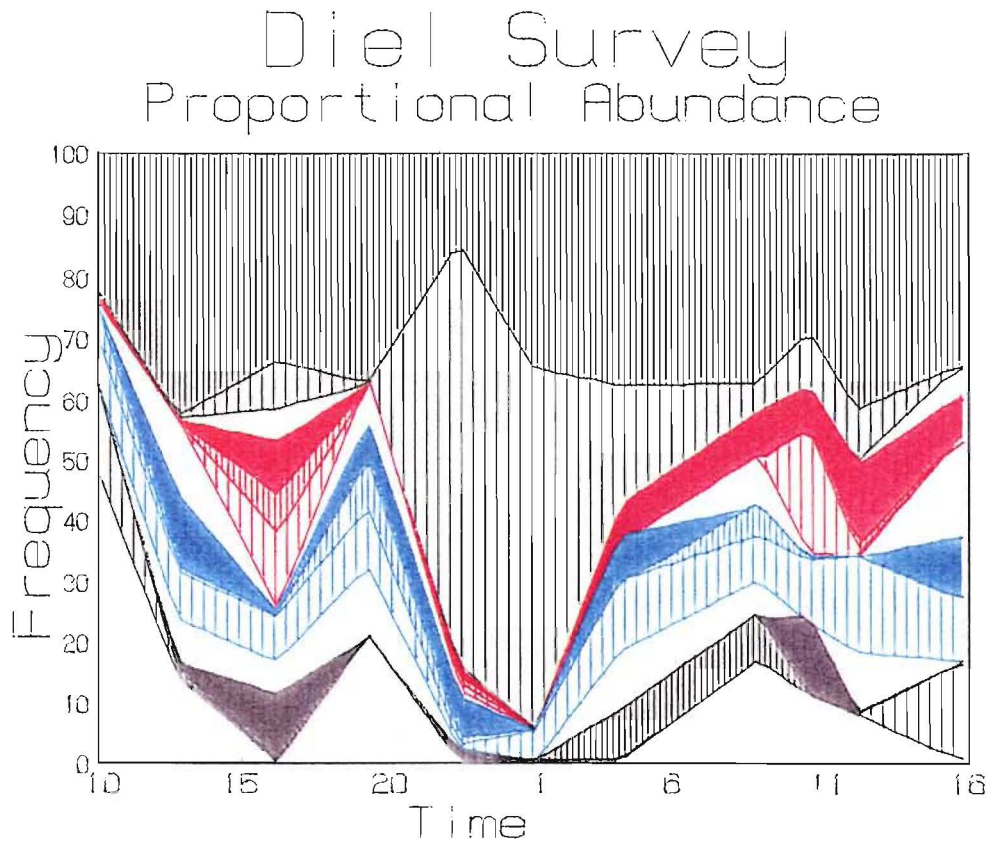


Fig. 20.

B.nauplii C. nauplii Cyprids Zoeae
Tornaria Gastropods Bivalves *Acartia*
Euterpina Ostracods *Daphnia* *Paralya*
F. larvae Fish eggs Others

ranging from 23-28 taxa and all species had low abundances. Changing tidal regimes and daylight periods were recorded with low species abundances and high species diversity duing these periods.

The fourth cluster in the dendrogram comprised periods C, I and J. These samples were all taken near midday; 4:10pm, 10:30am, and 12:10pm respectively. Tidal flow seems unrelated to this cluster, as nearly all states are represented in the group. Species diversity in these clusters ranged from low to high; 19, 20 and 27 respectively.

Species

Species clusters were produced using species abundances in the sample time dimension. Three main clusters have been produced by this method (Fig. 21). All groups contained a wide range of taxa, collected at different times of the day at varying tide conditions. These clusters appear to be more tightly associated than those produced for the sample periods, but do not correlate well with any of the major variables tested.

The first cluster is not really a cluster per se, but a loosely linked chain of quite dissimilar species. These taxa are: Pluteus larvae, cryptoniscid isopod larvae, ctenophores and fish eggs, *Simocephalus vetulatus* and *Halectinosoma* sp. These species can be found in singularly differing habitats. Some of the species have widely fluctuating abundances. Of these *Simocephalus vetulatus*, for example, was completely absent most of the time and fish eggs were occasionally numerically dominant.

Fig. 21 Cluster analysis of sample total zooplankton abundances during diel survey.

Percent chaining = 38.46

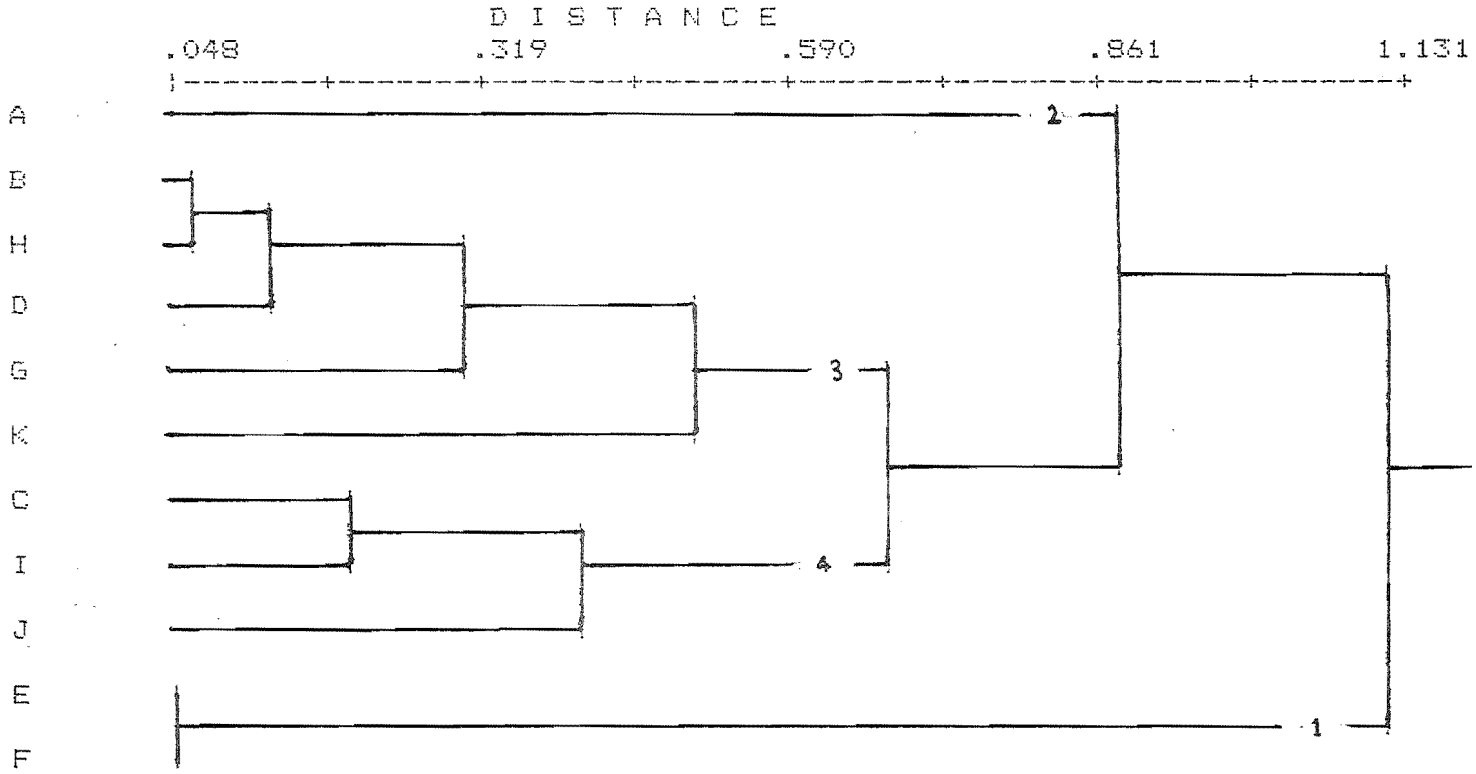
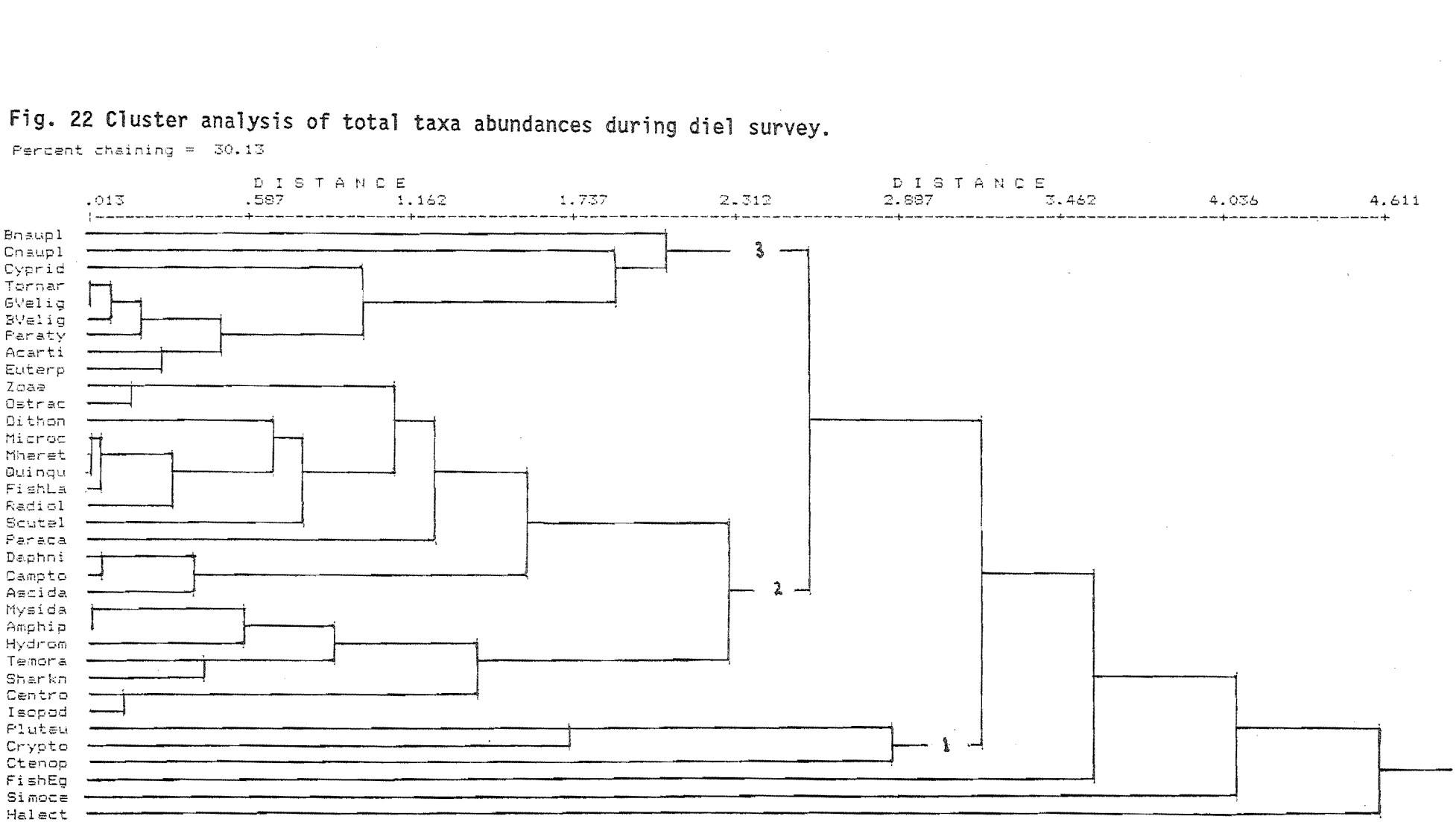


Fig. 22 Cluster analysis of total taxa abundances during diel survey.



The remaining species subdivided at a relative distance of 2.410 into two groups of 20 and 9 taxa respectively. The second cluster of 20 taxa comprised species from all sources, resident estuarine species such as decapod zoeae and *Miscegenus heretunga* and freshwater taxa like *Daphnia carinata, Camptocercus* sp. and an ostracod. Also included were taxa from coastal sources such as *Oithona similis, Paracalanus indicus* and Radiolaria. The remaining taxa in this cluster were *Microcyclops* sp. *Quinquelaophonte* sp., fish larvae, *Scutellidium* sp., Ascidacean larvae, *Tenagomysis* sp., Amphipoda, Isopoda, Calypto (Hydro) medusae, *Temora turbinata, Centropages aucklandicus* and a sharknose harpacticoid copepod.

The third group of 9 taxa produced in the cluster analysis included the most abundant taxa and thus these taxa were all numerically dominant during one period at least. These nine taxa were: barnacle nauplii, copepod nauplii, barnacle cyprids, gastropod and pelecypod veligers, *Paratya curvirostris, Euterpina acutifrons, Acartia* sp., and polychaete tornaria larvae.

Ordination

Bray-Curtis ordination techniques produced better correlations with environmental variables than site cluster analysis. This method accounted for large amounts of the sample variance.

Periods in Species Space

Following ordination variance explained by axes one to four was 31.6%, 23.8%, 13.2% and 10.3% respectively. Axes one and two accounted for over 50% of the sample variance and the ordination scattergram shows four clusters (Fig. 22). Correlations of the two axes with environmental variables were the inverse of turbidity for axis one (r=-0.291) and chlorophyll a concentration (r=0.516) for

axis two. These axes correlated well with biological variables of species abundance and correlation coefficients show that axis one was best described by samples with decreasing fish egg abundance (r=-0.796). Axis two was best described by samples with increasing concentrations of herbivorous copepod nauplii (r=0.744).

Species in period Space

Bray-Curtis ordination using Jaccard's distance measure and regression endpoint selections were made along four axes. These accounted for 9.1%, 15.6%, 8.9% and 5.7% of the sample variance respectively. The first two axes were used to distinguish species clusters which were clear enough to obviate the use of axes three and four. The plot produced by this analysis, (Fig. 23) also confirmed the findings of the previous cluster analysis. Axis one had the best correlation with species abundances during period C, 4:20pm (r=-0.266). Axis two correlated best with species abundances in period J, 12:30pm (r=-0.737). This period was a midday, ebbing tide with medium taxa diversity (20 taxa present) and low taxa abundances (five percent of total taxa abundance equals 37.23).

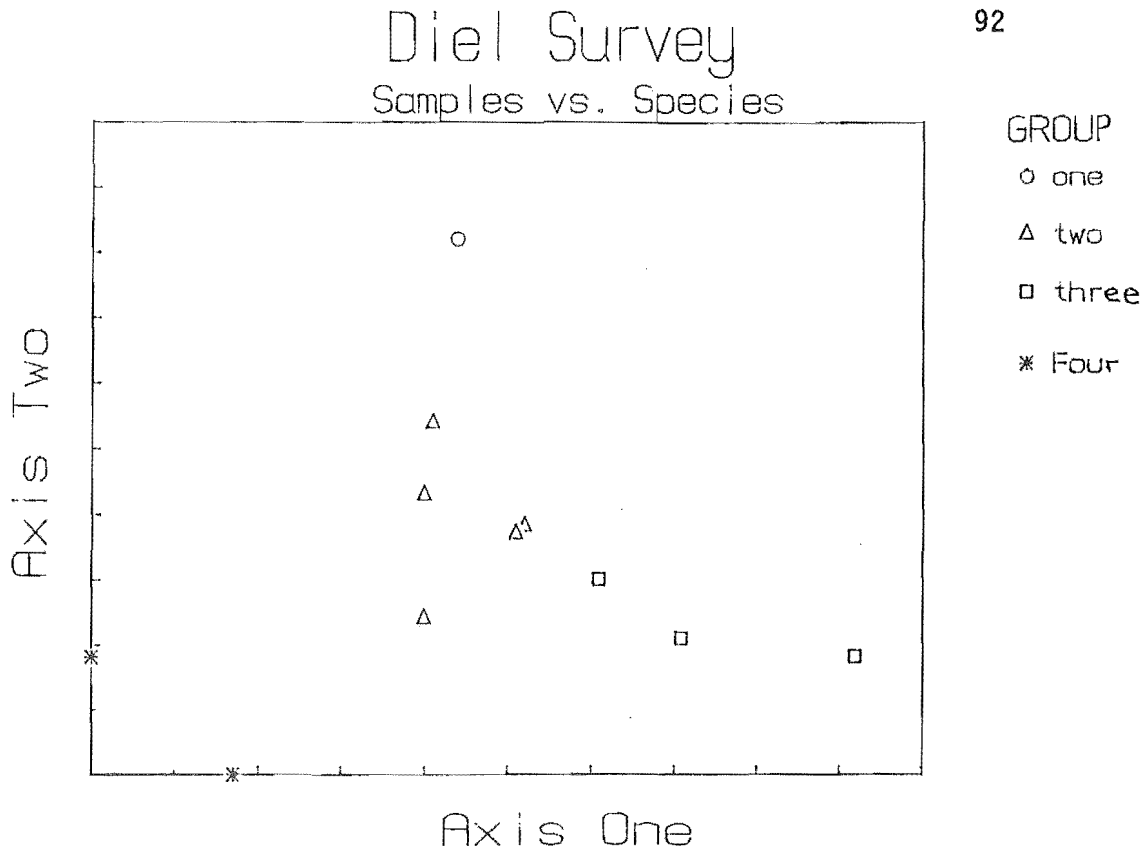


Fig. 23 Bray-Curtis ordination plot of samples from diel survey in Brooklands Lagoon using total zooplankton abundances.

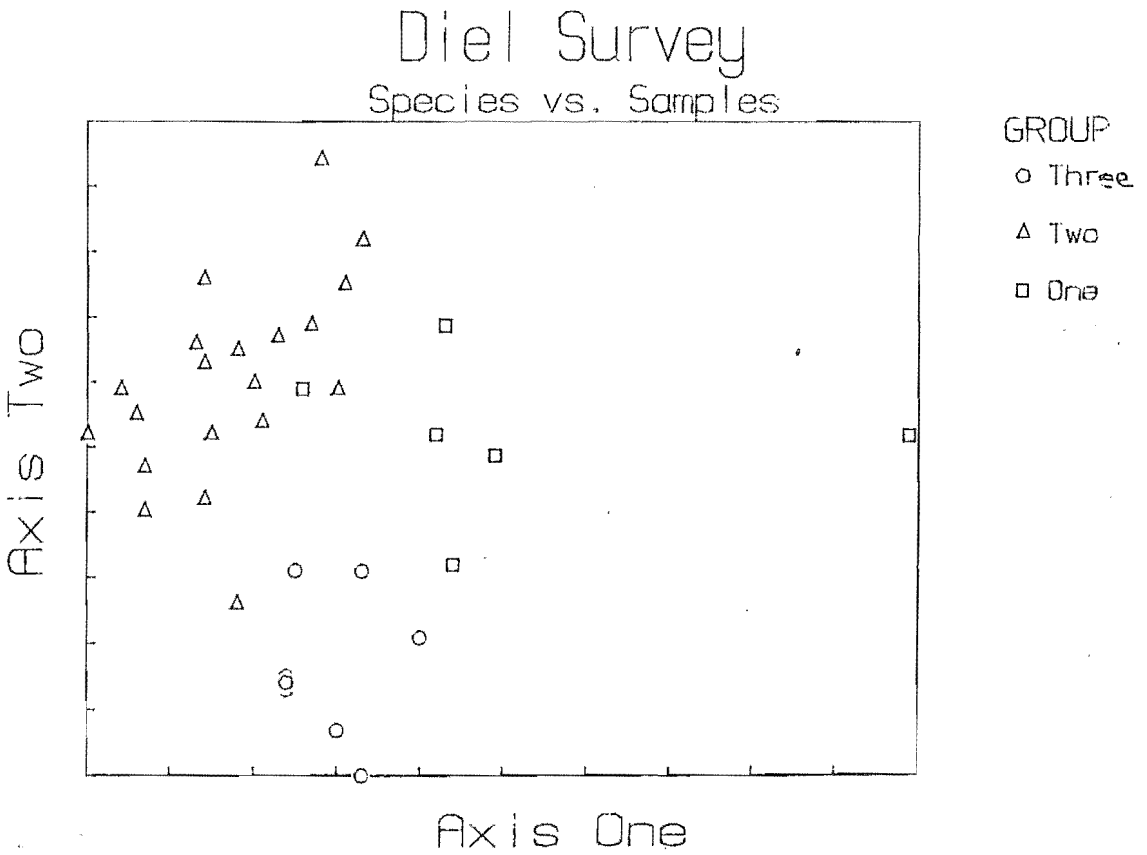


Fig. 24 Bray-Curtis ordination plot of taxa abundances from diel survey in Brooklands Lagoon using sample groups.

DISCUSSION

PHYSICO-CHEMICAL VARIATION

During the course of this study, most physico-chemical parameters showed regular fluctuations. Tidal ebb and flow was the most predictable of these and showed a regular diel, lunar periodicity and amplitude. Other factors were influenced by the tide. The most obvious of these was the turbidity which is due to floculation of silt particles. This is caused by the change of pH at the freshwater, seawater interface (Riley 1967, McLusky 1981). As tide flows into the estuary, floculation increases, increasing the water turbidity. An increase in the total zooplankton abundance could also be expected to increase the water turbidity (Bougis 1976). The lower turbidity peak reading at 11:00am occurred at the same time as a drop in zooplankton abundance (Fig. 19).

Although more complex, salinity varied with the tidal flow. However this factor is also affected by the water temperature such that when temperature increases, salinity decreases. Temperature changes, along with freshwater flooding and bathymetric retention times (Knox & Bolton 1977), may account for departure from perfect unison with the tide. Salinity therefore tended to lag behind the more regular tidal periodicity. Salinity may also affect directly the total zooplankton abundance.

During the tidal cycle it would be expected that the high tide would flush the estuary with increased amounts of zooplankton, increasing the biological oxygen demand (Jeffries 1962a). This in turn would depress the amount of dissolved oxygen due to demand by the non-photosynthesizing animals while dissolved oxygen is not being replaced immediately.

Other periodicities of phsico-chemical factors were present. Chlorophyll a concentration, which is an indirect measure of phytoplankton concentration (Fig. 17) showed a daily rise and fall. Chlorophyll a concentration followed in unison with the photoperiod, rising during the day and falling during darkness.

Temperature was another factor closely associated with the photoperiod. During the day temperature rose as sunlight heated the water. The heatsink properties of water are well illustrated by the temperature curve (Fig. 17) which showed that the temperature did not decrease until well after sundown and did not rise until well after sunrise.

Oxygen concentration was generally very high in the estuary waters. This implies that oxygen is unlikely to limit the zooplankton abundance. There was a significant decrease at the start of the second day. This change could reasonably be attributed to the lack of phytoplankton activity during the preceding hours of darkness. At the same time the rising tide flushed the estuary increasing oxygen levels. Both of these events would depress the dissolved oxygen concentration and together they make a significant impact. Oxygen concentrations were quickly restored to high levels at the start of the new day enabling phytoplankton to photosynthesize.

Abundance

Total zooplankton abundance followed a predictable series of changes as described by Deevey and Brooks (1971). Abundance decreased during periods of ebb tide and increased with the flood tide during the day (Fig. 19). At night this pattern was obscured by other distribution factors. Benthic species from the estuary emerge during total darkness, swelling the numbers of zooplankton normally present. With the rising moon and ebbing tide there was a decrease in

zooplankton abundance. However the zooplankton abundances did not decrease to daytime levels during the nightly low tides, but remained as high as daytime high tide abundances. With the sunrise zooplankton abundance fell dramatically even though there was a flood tide. This may be explained by depressed concentrations of chlorophyll a following the night (Hardy 1956). Many of the zooplankton found in the estuary are herbivorous and the stronger swimmers swept in from neritic sources may be repelled by decreased salinities of the river water. Perhaps zooplankton show an attraction for higher concentrations of phytoplankton regardless of salinity. This effect might cause an overall zooplankton movement towards the river mouth during daylight as these areas would appear attractive concentrations of food to zooplankton due to terrestial runoff.

The opposite pattern of abundance was also exhibited by the larvae of the resident crabs. Brachyuran zoeae were more abundant during the low tide periods. Swimming behaviour of such estuarine species causes them to rise in the zooplankton during the flood tides, making them more dispersed but sweeping the zoeae up the estuary preventing population distribution drift out of the estuary. During ebb tides these species congregate near the bottom in estuaries as a mechanism to avoid the stongest ebb flows at the surface (Sandifer 1975).

Composition

During the hours of daylight the average abundance of zooplankton was lowest and taxa diversity was highest. In the period of total darkness, when zooplankton abundances were greatest, there were only three dominant zooplankters. These are primarily, fish eggs and also, *Acartia* sp. and gastropod veligers. Increased nightly

abundances are a reflection of the diel abundance patterns described by many researchers (Deevey 1960a, Hardy & Gunther 1935, Ewald 1912, Barnes 1926). My results support the theory that zooplankton distribution within the water column is a phototaxic response (Ewald 1912). In complete darkness zooplankton would always swim upward according to this theory. These animals would then have high surface abundances as happened in this study. My results suggest that very little light is necessary to scatter zooplankton down into the water column. Moonlight, which was the only variable to change at the time, appeared to significantly reduced abundances. Later in the morning, following sunrise, zooplankton appeared completely scattered to minimal abundances. Even though the tide was rising at 4:00 hours on the second morning zooplankton abundances continued to fall. This effect can only be explained by rising light intensity (Ewald 1912), or falling concentrations of chlorophyll a (Hardy 1956). However there were no increases in zooplankton abundance during the previous daytime low tide when chlorophyll a concentrations were high. This trend was reversed in the early evening when zooplankton abundances were high during low tides at the same time that light intensity was low and chlorophyll a concentration was high. Therefore the evidence from this survey supports Ewald's theory that the zooplankton diel migration is due to a phototaxic response.

At midday the zooplankton included barnacle nauplii, brachyuran zoeae, gastropod veligers, polychaete tornaria, fish eggs and fish larvae and the dominant holoplankton were replaced by freshwater species, for example *Paratya curvirostris* and the ostracods. This may have been due to freshwater flow from the Styx river through site two at low tide, but cannot be tested.

Bray-Curtis ordination of sites grouped by cluster analysis show clusters along axes best described by water turbidity wich is a measure of light penetration, for axis one (r=-0.291) and chlorophyll a concentration for axis two (r=0.516). When the species ordinations were overlayed on the first plot nearly all have abundances distributed in regions representing medium to low light intensity. However the second axis spreads the distributions over a range of daily chlorophyll a concentration.

The species clusters showed that group one consisted of mostly larvae such as nauplii and copepodites, which prefer medium light intensities (Bougis 1971). This group appeared to be able to utilise lower chlorophyll a concentrations as shown by their postion on the second axis.

Group two were adult species preferring the darkest situation using medium chlorophyll concentrations. Estuarine species are usually found in such conditions as they are able to use less concentrated food sources compared to the more competitive stenotaxic marine species (McLusky 1981). In neritic waters their feeding rates may be less competitive, however this disadvantage may be offset by their increased tolerences to salinity fluctuation in estuaries.

Group three were generally adult individuals of larger biomass, which appear during daylight hours. These individuals might be expected to be feed more efficiently on higher chlorophyll a concentrations (refer appendices). To off set the disadvantage of increased visibility to predators these animals may feed in turbid waters decreasing their visibility to predators. This effect is seen placing them in medium light distributions within the ordination.

The final cluster of species did not have enough information to classify them biologically. However these animals were generally weaker swimmers or complete drifters, less able to position themselves, in the water column. They sometimes appeared in high abundances in bright light conditions. For example the ctenophores which have phototaxic redia and are carnivorous. Also in this group were the highly abundant fish eggs which have no swimming ability.

CONCLUSIONS

Within Brooklands Lagoon daily fluctuations of zooplankton abundance are dependent mainly on the photoperiod. This environmental factor alone influences several others such as phytoplankton production and temperature. Secondary factors are, in order of importance, tidal regime, chlorophyll a concentration, temperature and dissolved oxygen concentration.

Zooplankton have daily changes of abundance due to vertical migration in response to light strength as first suggested by Ewald (1912). Chlorophyll a concentration (an indirect measure of phytoplankton abundance) is not an important feature causing vertical migration in summer in Brooklands Lagoon as suggested by Hardy (1956).

CHAPTER FOUR

ZOOPLANKTON BIOMASS

INTRODUCTION

Representing community structure by numbers of individuals of each species assumes that all species have the same size and weight. However zooplankton may range in size from nauplii weighing a few micrograms to ctenophores and medusae several cubic centimetres in length and several grams in weight. Population biomass is a better indication of the food available to upper trophic levels.

A generally understood ecological trend is the tendency for organisms occupying lower trophic levels to be smaller and more numerous (Odum 1971), but numbers of each species alone give little indication of the biomass available to the next trophic level. Biomass estimates provide information on the potential energy flow through the ecosystem. However due to assimilation inefficiencies usually only approximately 8-10% of the available energy value at one trophic level may be transferred to the next (Slobodkin 1960, Odum 1971). The general principle of 10% energy transfer between trophic levels leads to a pyramid of decreasing biomass at successive trophic levels. Highest trophic levels are likely to contain fewer individuals with a larger body mass.

Marine food chains tend to be longer than terrestial or freshwater examples (Newell & Newell 1973); they therefore require higher biomass at lower trophic levels. Because zooplankton are generally near the base of marine food chains this implies that a well balanced ecosystem will have a relatively large amount of zooplankton biomass, or these animals will have a high production rate. A measure of biomass may be a better indication of the ecological status of the zooplankton within Brooklands Lagoon than

numbers alone. The aim of this chapter is to measure the contributions of zooplankton to the food web within Brooklands Lagoon by estimating the biomass present. The results from seasonal and diel surveys will indicate the availability of the zooplankton as a permanent or temporary food supply for higher food web levels.

METHODS

Samples collected for the seasonal samples were used to estimate zooplankton biomass in Brooklands Lagoon. Enough individuals of each species were collected to give a total dry weight of at least 10ug and these were used to obtain estimates of the average individual dry weights. Individual taxa were washed in distilled water, filtered on to gauze and dried in an oven at 60°C. The samples were then kept in a desiccator for one hour to allow the temperature to stabilize and prevent moisture uptake before they were weighed on a Cahn microbalance.

Dry weights obtained by this method were then used as conversion factors for the biomass of each species. Biomass values were calculated for each species from the seasonal survey results described earlier. They were then used in community cluster analysis and Bray-Curtis ordination, using Jaccard's distance measure and Euclidean geometry.

RESULTS

Seasonal

Seasonal and spatial distribution of those species comprising more than 5% of the total biomass are shown in figures 25-27. These species were barnacle and copepod nauplii, barnacle cyprids, *Acartia* sp., *Microcyclops* sp., *Miscegenus heretunga*, *Camptocercus* sp., *Paratya curvirostris* and fish eggs, representing 71-93% of the

biomass at sites two and 38-94% at site three. None of these species exhibited continuous dominance of the biomass, but nearly all showed presence throughout the year. Some species were present at all sites but only represented within the dominant biomass at a single site such as *Temora turbinata* at site one, *Paracalanus indicus* at site two and brachyuran zoeae at site three. These less widespread species were also present at each site for shorter periods. *Temora turbinata* was dominant only in June; *Paracalanus indicus* was dominant in January, June, August and October; while brachyuran zoeae were found during December and November only.

A few of the species more widespread throughout the estuary also occurred for shorter periods. *Paratya curvirostris* was included only during December and January. Tornaria were present at all three sites during August, site one in September, sites two and three in November and December and site two in March.

The most abundant components of the biomass within the estuary were the copepod and barnacle nauplii which were found at every site throughout the year. Copepod nauplii were included in the dominant fauna for short periods only during January, February and December 1986. Barnacle nauplii were nearly continuously dominant at sites two and three, but appeared only once in the dominant biomass at site one, in February.

Miscegenus heretunga was present in the dominant biomass in the estuary for intermittant periods. Its importance increased from the mouth to the head of the estuary. *Acartia* sp. showed the same changing pattern of dominance increasing up the estuary, while copepod nauplii showed the opposite pattern.

g. 25 Proportional representation of taxa comprising more than 5% of zooplankton biomass at site one during a seasonal survey.

g. 26 Proportional representation of taxa comprising more than 5% of zooplankton biomass at site two during a seasonal survey.

Seasonal Biomass

Site One

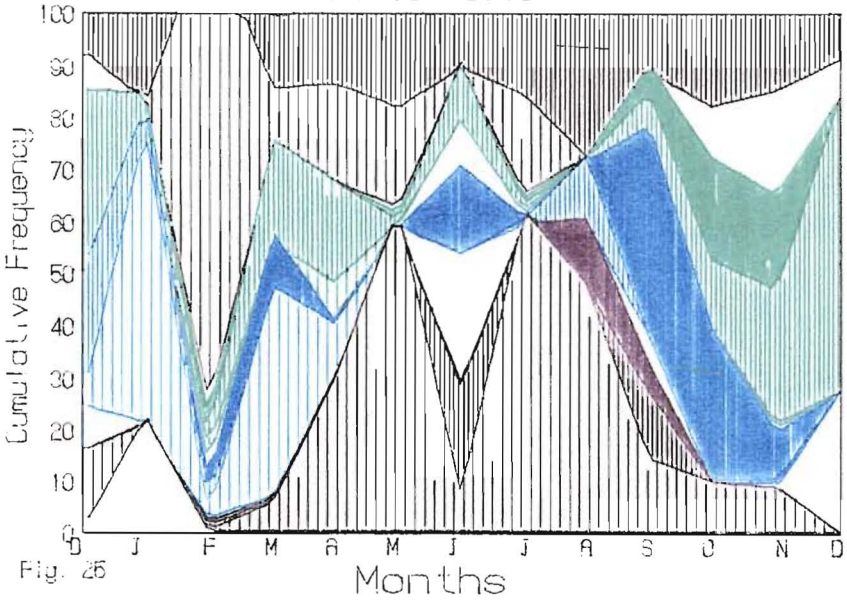
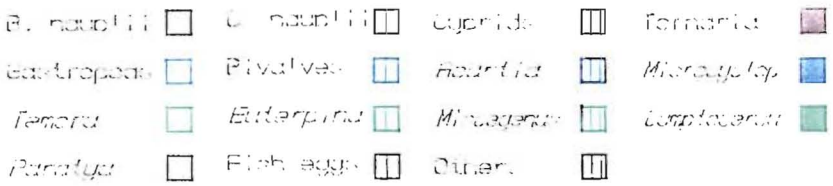
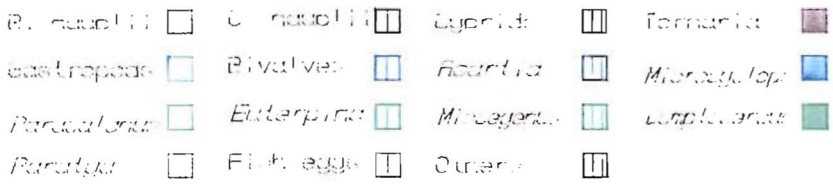


Fig. 25





Seasonal Biomass

Site Two

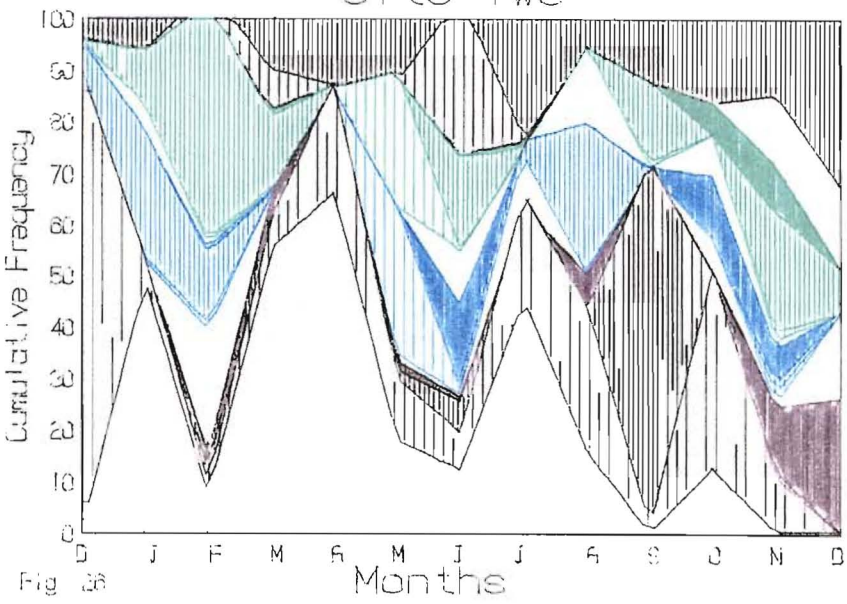


Fig. 26

27 Proportional representation of taxa comprising more than 5% of zooplankton biomass at site two during a seasonal survey.

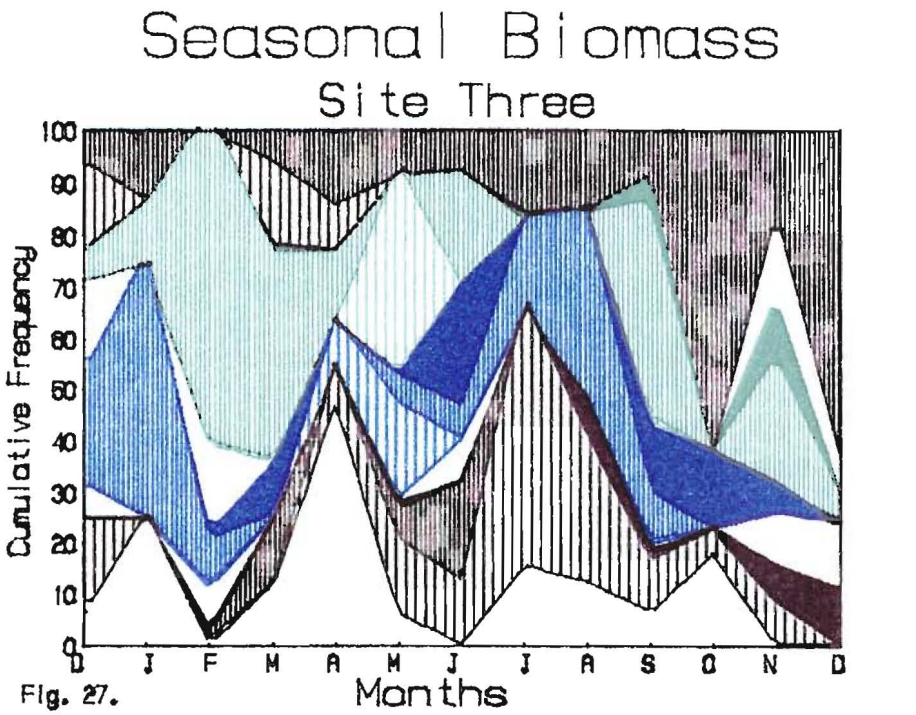

Seasonal Biomass
Site Three
Cumulative Frequency
100
90
80
70
60
50
40
30
20
10
0
J F M A M J J A S O N D
Months
B. nauplii
C. nauplii
Cyprids
Tornaria
Gastropods
Bivalves
Acartia
Microcyclops
Paracalanus
Eurterpina
Miscegenus
Camptocercus
Paratya
Fish eggs
Others

Fig. 27.

Some common species were not represented in the dominant biomass although their dry weights were relatively high and their numbers were sometimes high. These taxa include *Oithona similis*, bivalve veligers, mysids, ascidean and fish larvae.

Cluster analysis

Seasonal site cluster analysis formed five major clusters at a relative distance of 4.41 (Fig. 28). The first cluster was a single sample from site one in February. This period had the warmest temperatures and was strongly influenced by unseasonal flooding frequency causing high river flows (Fig. 4).

The remaining data split into two major clusters at a distance of 3.997 producing group 2 (Fig. 28). This group contained samples at sites less affected by high river flows and flood action, that is sites two and three. Samples in group 2 from site one were from months of relatively fewer floods compared to river flow: January, May, July and August (Fig. 4).

The remaining samples subdivided at a relative distance of 3.648. Group 3 (Fig. 28) contained samples taken from site one during winter and spring, which all had low zooplankton abundances (Appendix A). The final samples subdivided at a distance of 3.377, forming clusters 4 and 5 (Fig. 28). Cluster 5 contained samples with relatively high abundances during summer. At this time water temperature was highest and chlorophyll a concentration was quite low. This separation left cluster 4 which contained all the samples taken during spring at all sites, except those from site one in September and October. Cluster 4 represented a group of samples taken during the highest Waimakariri River flow periods and when flooding was most frequent, salinity very low and turbidity high (Fig. 7). There were also high concentrations of chlorophyll a (Fig. 8). An

outlier from this group which later formed a single cluster (Fig. 28) was the site two sample in September. This sample had a very low chlorophyll a concentration of 41 g/l (Fig. 8).

Site one samples within cluster 2 represented a group of outliers which later clustered apart at a relative distance of 2.756. An exception in this case was the sample from site one in January. This sample was taken at a time of high salinity, low river flows and low flood frequencies.

Cluster analysis of species formed four major clusters (Fig. 29). The first cluster divided at a relative distance of 3.949. This cluster contained *Centropages aucklandicus*, *Daphnia carinata*, *Temora turbinata*, *Oithona similis* and *Tenagomysis* sp. which were all relatively rare in the seasonal samples. Of these *Daphnia carinata* and *Tenagomysis* sp. inhabit fresh or brackish water and the others are neritic marine species.

The species split again at a relative distance of 3.516, forming group 2 (Fig. 29) containing *Paratya cuvirostris*, *Microcyclops* sp., *Camptocercus* sp. and the ostracods. These are all freshwater inhabitants with low abundances. The final clusters, groups 3 and 4 (Fig. 29), at a relative distance of 2.278. Group 3 contained barnacle cyprids, gastropod veligers, brachyuran zoeae and fish eggs which are all meroplankters of euryhaline marine species. The last cluster contained barnacle and copepod nauplii, *Acartia* sp., *Miscegenus heretunga*, *Euterpina acutifrons*, *Paracalanus* sp., bivalve veligers and tornaria larvae, the most abundant species in all the samples and all have been recorded as euryhaline, marine or estuarine inhabitants (Hicks & Coull 1983, Moreira et. al. 1982, Jeffries 1962a).

Fig. 28 Cluster analysis of total monthly sample zooplankton biomass in Brooklands Lagoon.

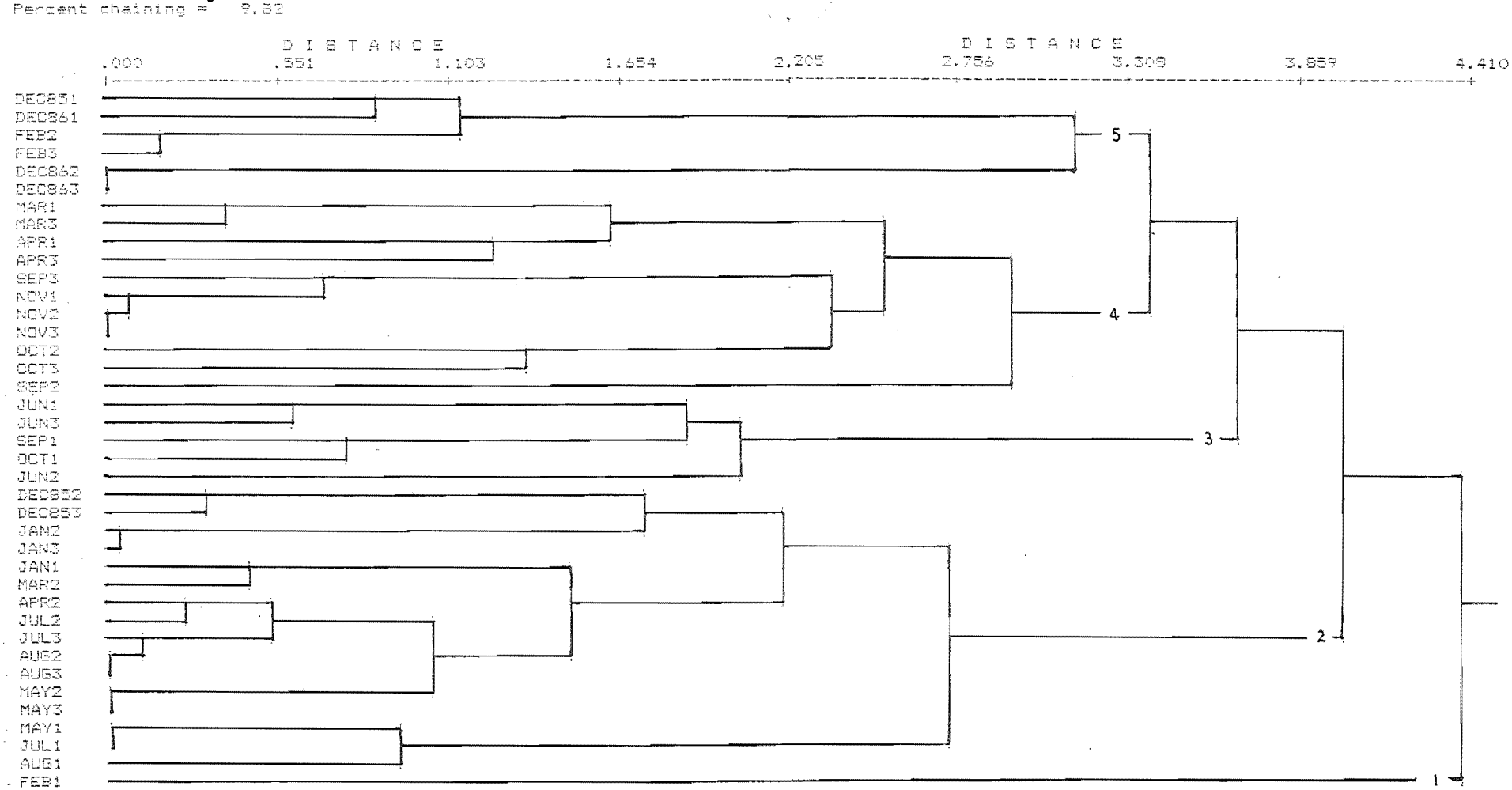
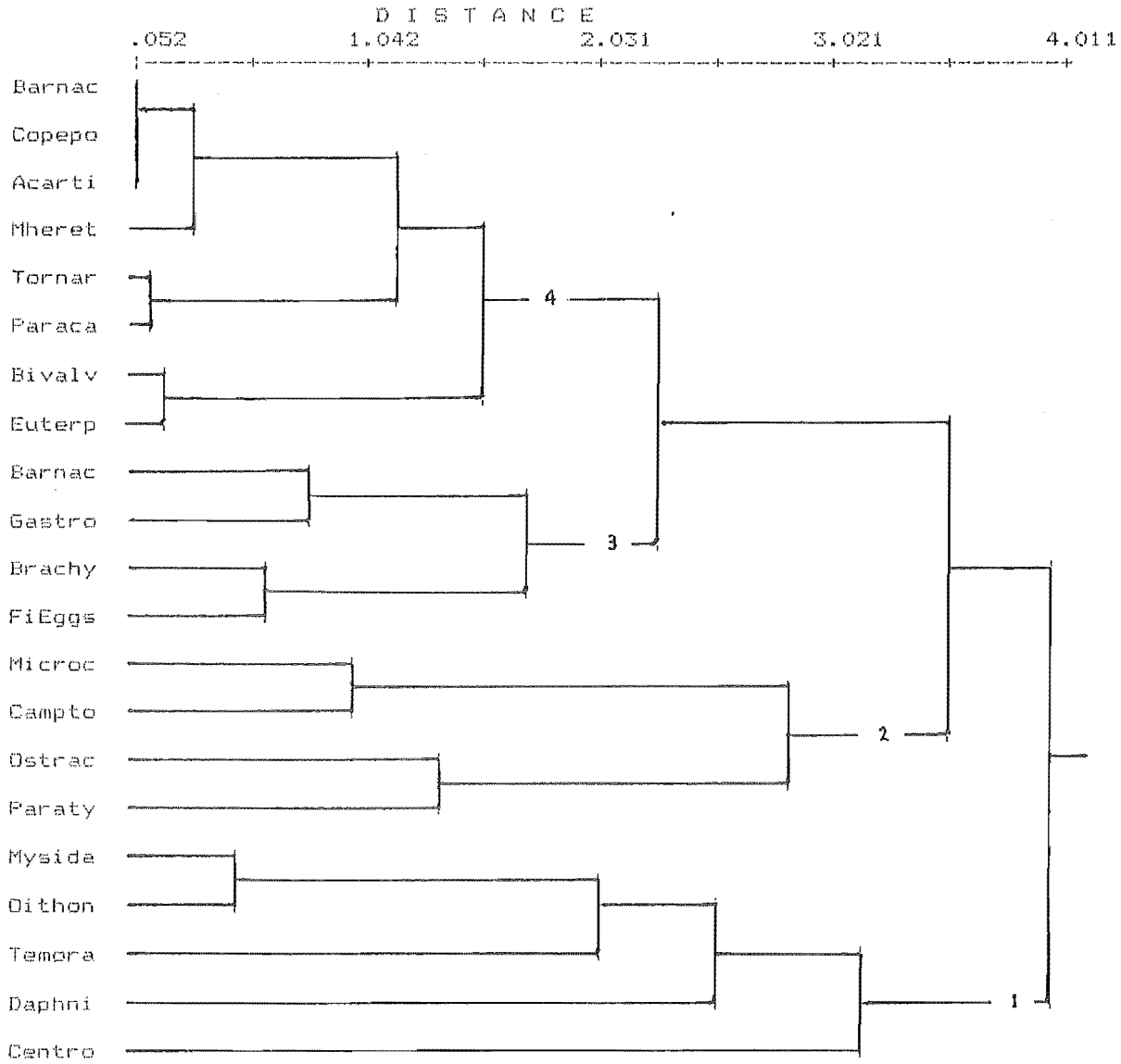


Fig. 29 Cluster analysis of total taxa biomass in Brooklands Lagoon.
Percent chaining = 8.82



Ordination

For the ordination of biomass from each site in species space, the first four major axes explained 16.8%, 6.7%, 4.9% and 5.7% of the data variance respectively. Only axes one and two, explaining the most variance, were used for interpretation (Fig. 30). This plot shows that group 2 from the cluster analysis is distinctly separated from the remaining samples. The other clusters were all formed inside the boundaries of cluster five and appear as subsets of this group. Correlation coefficients for axis one showed the best association with the inverse of tidal periodicity ($r=-0.412$), which also showed a high degree of association with axis two ($r=-0.542$). Axis two showed some correlation with the inverse of flood frequency in the Waimakariri River ($r=-0.311$) as well.

The ordination of species biomass within site space produced four axes explaining 11.9%, 8.3%, 6.4% and 6.6% of the variance respectively. Once again only axes one and two were used for the ordination plot (Fig. 30). This plot showed that the clusters from previous cluster analysis separated well within ordination space along axis one. Groups 1 and 2 ordinated in space where samples had less tidal influence and medium to low flood frequency when overlaid on the ordination of sites in species space (Fig. 30). Clusters 1 and 2 were not well defined with some overlap in the second dimension. Both of these groups have overlaid areas of medium to high tidal flows and contain animals from distinctly marine or freshwater habitats.

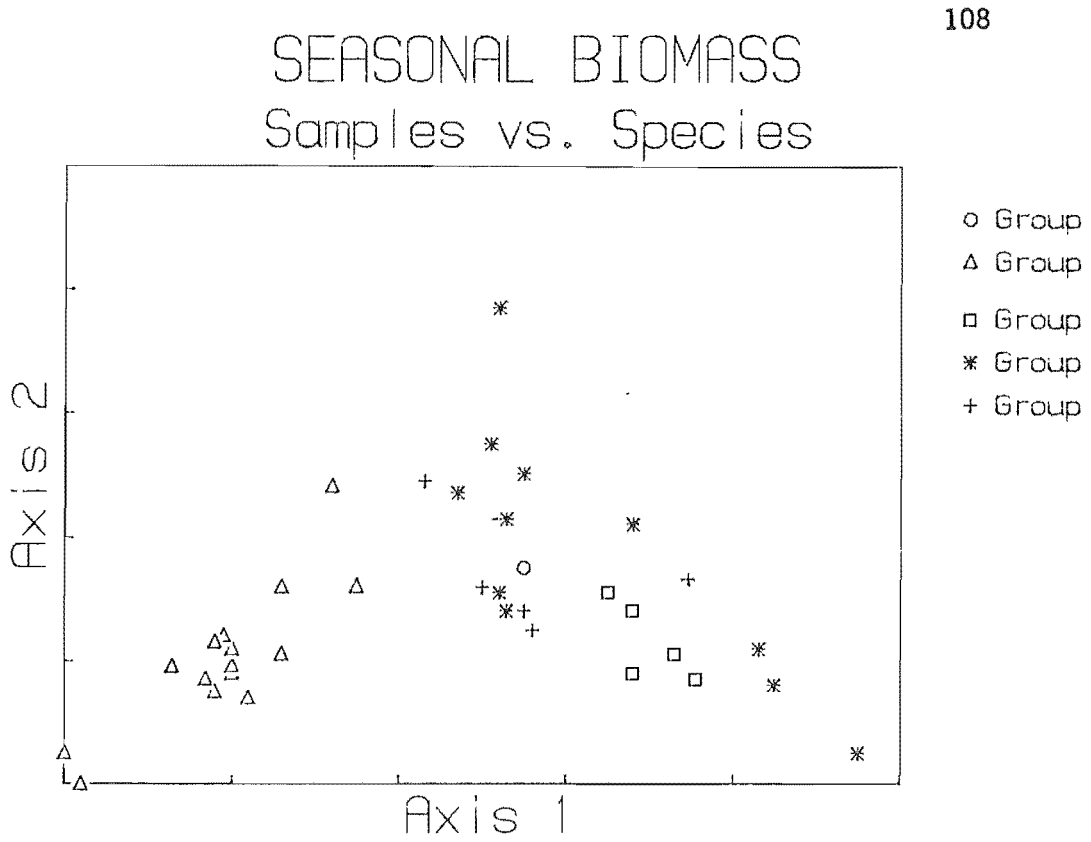


Fig. 30 Bray-Curtis ordination of total zooplankton biomass data of all samples from Brooklands Lagoon.

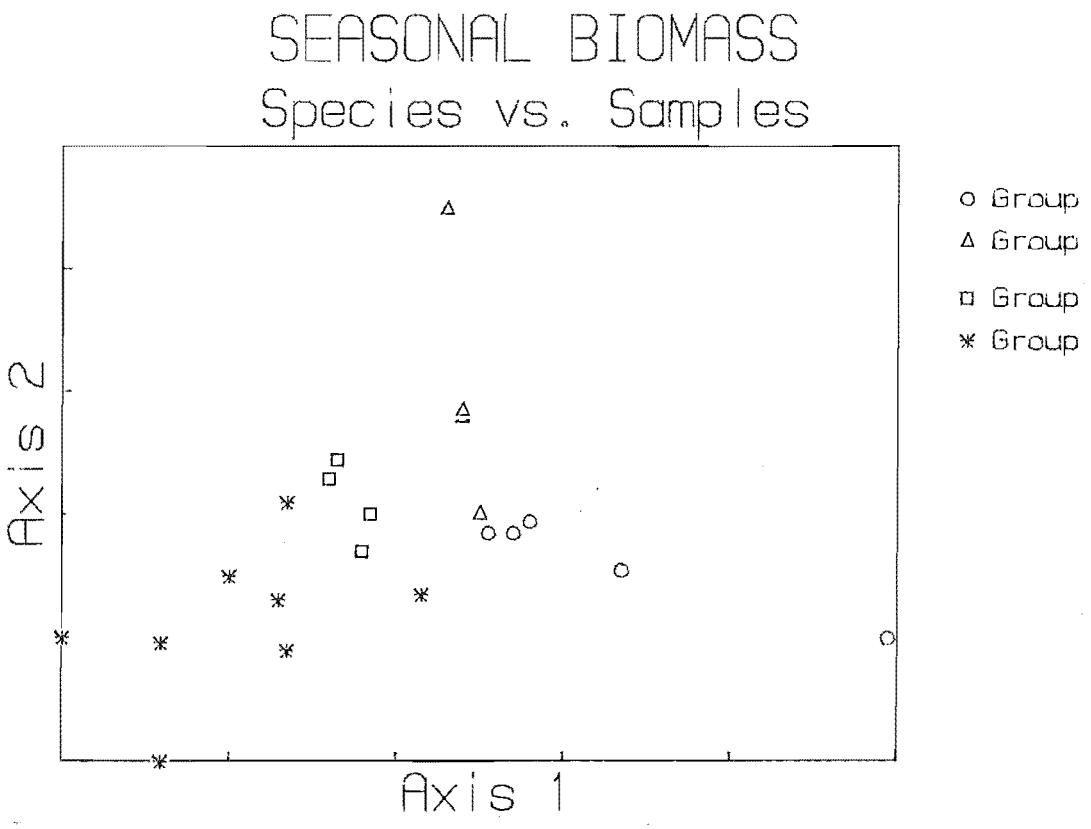


Fig. 31 Bray-Curtis ordination of taxa biomass data of all samples from Brooklands Lagoon.

Diel Survey

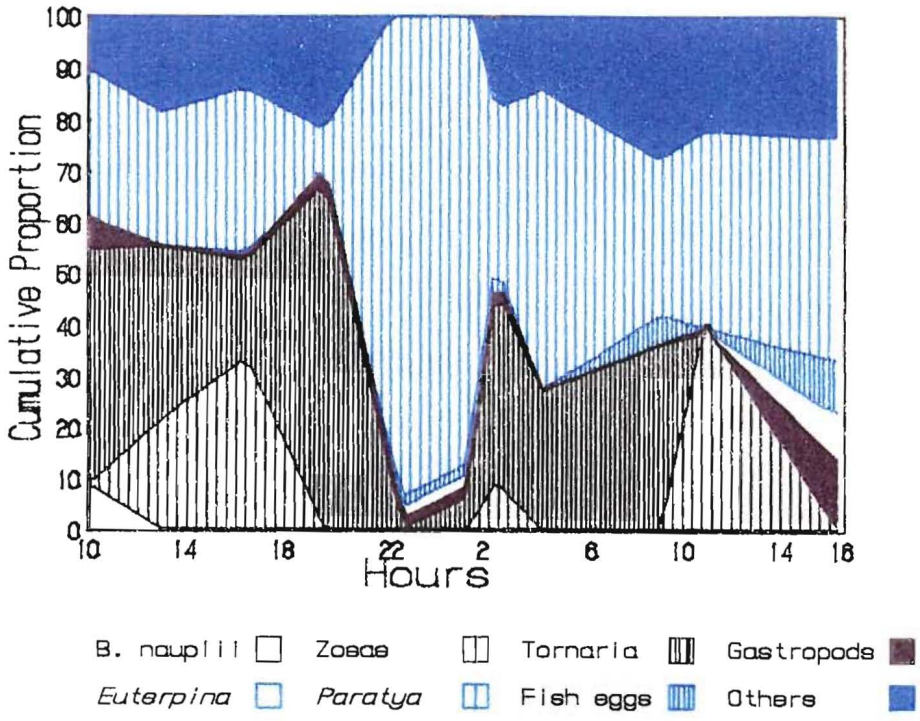
Only 7 of the 35 species found in the diel survey represented more than 5% of the total biomass. These were; Fish eggs, *Paratya curvirostris*, *Euterpina acutifrons*, gastropod veligers, tornaria larvae, brachyuran zoeae and barnacle nauplii (Fig. 31). Only three taxa were present continuously during this survey, tornaria larvae, gastropod veligers and fish eggs.

Barnacle nauplii were dominant during the first morning only. Later in the day their biomass and copepod nauplii were sometimes quite high, but never represented a major fraction (Appendix D). Some species, brachyuran zoeae, tornaria, *Paratya curvirostris*, *Euterpina acutifrons* and gastropod veligers showed increased biomass during daylight. Brachyuran zoeae represented the largest amount of biomass during the daylight, reaching 40% at midday, on incoming tides. During the night, these taxa represented by biomass values less than 5% of the total zooplankton, but never totally disappeared (Appendix D).

In every sample fish eggs formed a significant fraction of the biomass, with an average value of 40%. This proportion increased during the night to 95% while the moon was absent. The proportion decreased in the early morning before the sun rose. As the proportion of fish eggs decreased, tornaria larvae increased to form a major fraction of the zooplankton biomass, corresponding with the flood tide, and sunrise. During the next day, on the high tide, tornaria were replaced by brachyuran zoeae, which decreased with the ebbing tide at the same time biomass of gastropod veligers rose. As the water shallowed *Euterpina acutifrons*, a coastal, harpacticoid copepod represented a significant portion of the biomass while total biomass was low.

32 Proportional representation of species comprising more than 5% of the total zooplankton biomass at site during the diel survey.

Diel Biomass
Site Two



Diel Cluster Analysis

Eleven sample periods were clustered by this analysis, producing three possible classes of site clusters. However a high degree of chaining in this analysis (34.6%) indicated some ambiguity. Cluster distances were all very close, that is the longest relative distance was 1.09. The first cluster (Fig. 33) contained samples taken at 10:30pm and 1:30am. These were taken during the night at the darkest period. The second cluster contained samples from pre-sunset, 7:15pm and 5:00pm and before sunrise, 4:30am. These three samples had low salinity, low turbidity and ebb tides in common. The remaining samples in cluster 3 were all taken during daylight hours.

Species biomass clusters formed three major groups (Fig. 34). Group 1 separated at a relative distance of 3.089 and contained meroplankton forms present in every sample (Appendix D). These were fish eggs, brachyuran zoeae and tornaria larvae.

Group 2 formed at a relative distance of 2.273 and contained a mix of meroplankton and holoplankton. These animals derived from freshwater, estuarine and marine sources and seemed to have no common environmental or biological association. The final cluster split into three parts; copepod nauplii may have been an outlying member of this group as they appear chained from the rest at a relative distance of 1.697. The other two parts were a group containing freshwater species (group 3) and another consisting predominantly of the copepods (group 4). The freshwater species in group 3 were *Daphnia carinata*, *Camptocercus* sp. and the ostracods. The exception in this group were the barnacle cyprids which are the cyprids of *Elminius modestus*, a euryhaline, sheltered aspect species. Group 4 contained the copepods *Oithona similis*, *Miscegenus heretunga*, *Centropages aucklandicus*, *Temora turbinata*, *Paracalanus indicus* and *Microcylops* sp. These

Fig. 33 Cluster analysis of total biomass from each sample during the diel survey in Brooklands Lagoon.

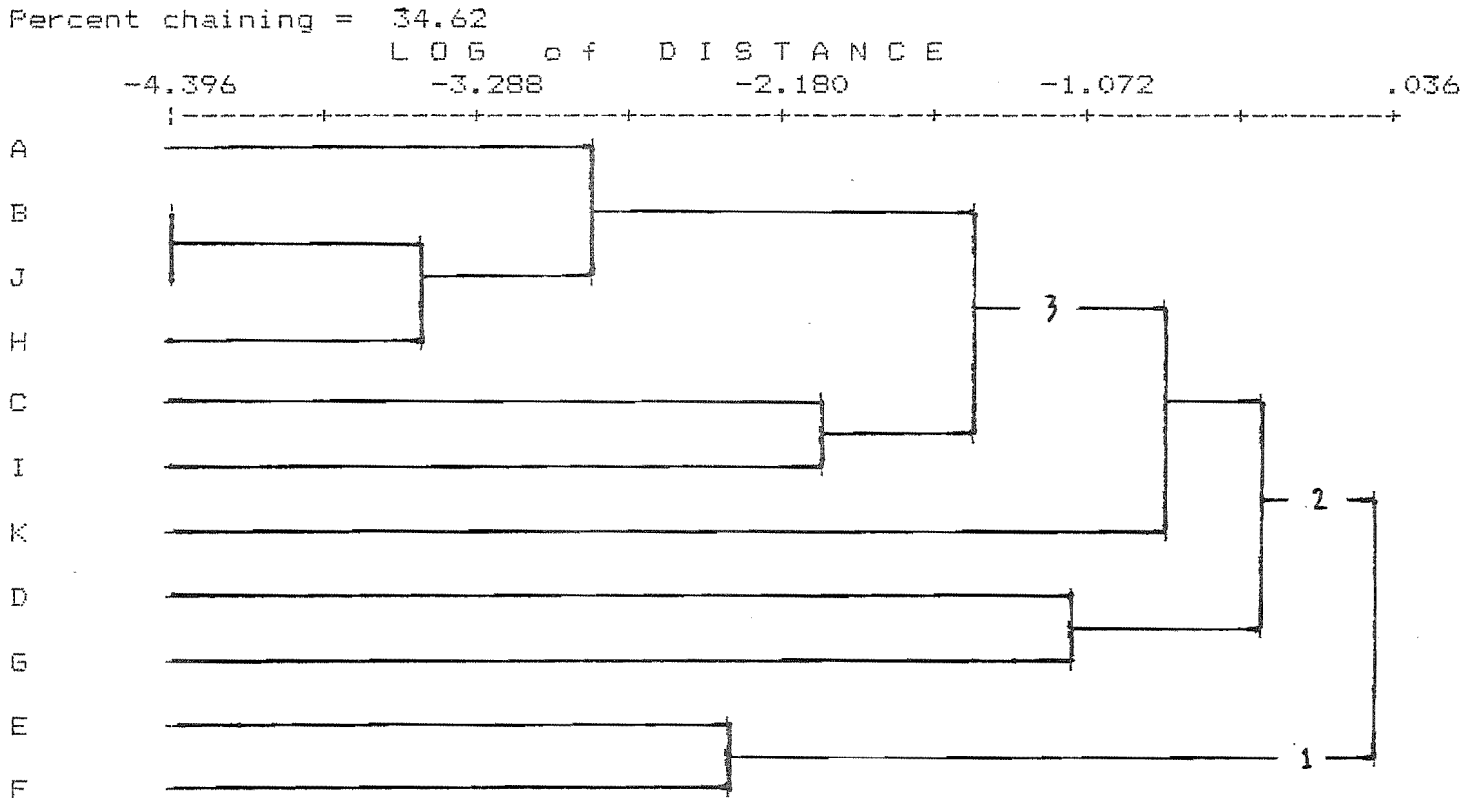
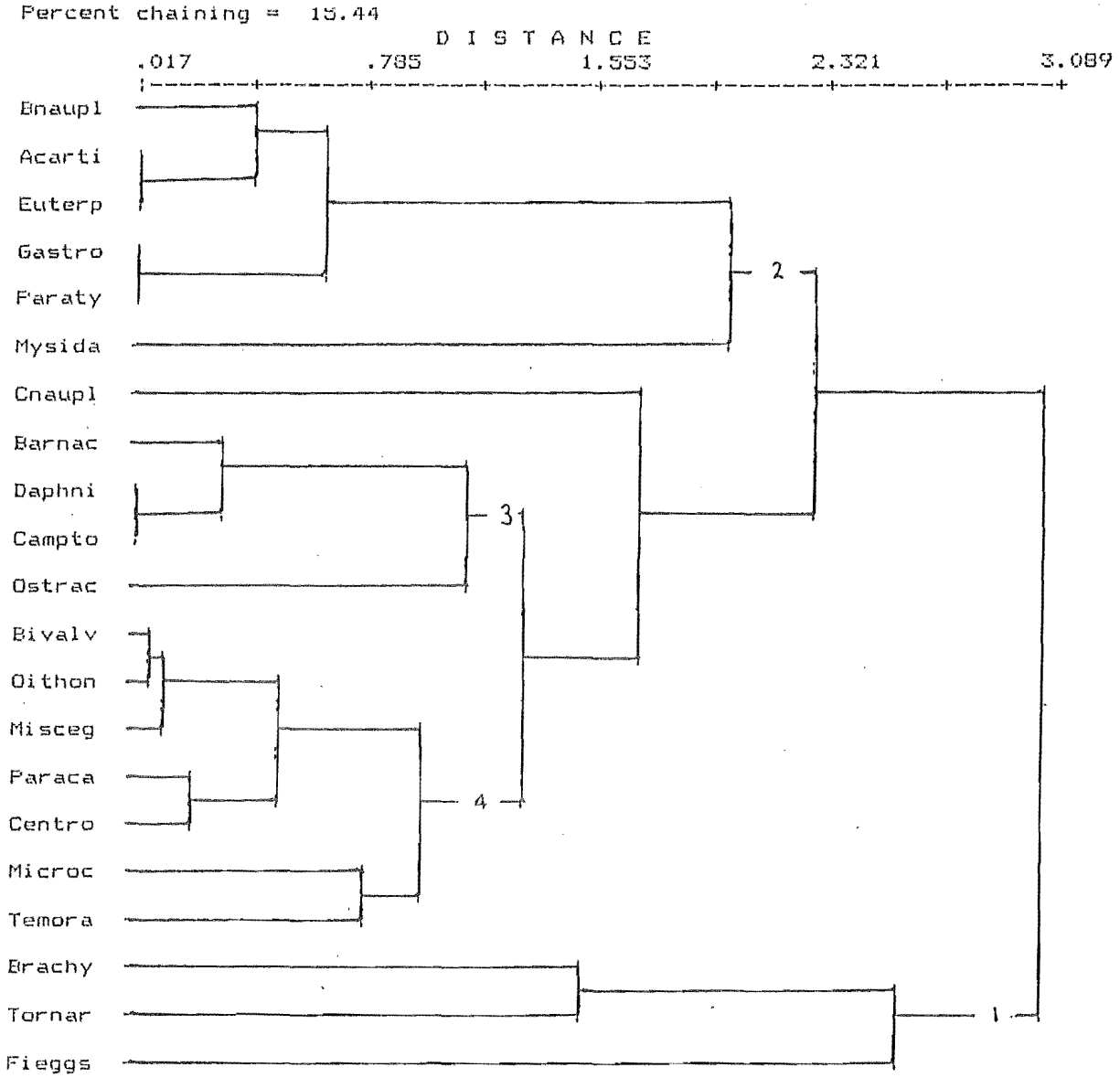


Fig. 34 Cluster analysis of taxa biomass from all samples during the diel survey in Brooklands Lagoon.



copepod species come from a variety of freshwater, estuarine, meiobenthos and neritic marine habitats. The exception in this cluster was the bivalve veligers.

Diel Ordination

Bray-Curtis ordination of samples in species space using Jaccard's distance measure produced four axes explaining 35.8%, 16.2%, 12.4% and 11.4% of the sampled variance respectively. Only axes one and two, explaining the most variance, were used to construct the ordination plot (Fig. 34). Axis one was correlated best with diel period (r=-0.584) and axis two with chlorophyll a concentration (r=-0.514). These axes have no units as they have been formed in hypothetical space (Fig. 35 and 36). Other correlations of secondary importance with axis two are temperature (r=0.461) and salinity (r=-0.425). The first cluster of samples E, 10:00pm and F, 1:30am, clustered to the right along axis one while the daylight samples from both days clustered left on axis one. Cluster group 2 was positioned in the centre of ordination space along axis one, but covered the whole range of axis 2.

Three axes were produced by ordination of species biomass in sample space, using Jaccard's distance measure and explained 15.4%, 10.5% and 9.4% of the sample variance respectively. Once again only the first two axes were used to construct the ordination (Fig. 35). The groups of samples produced in the preceding cluster analysis were distinctly separate in this plot. However group 4 appeared as a subset of group 3. When overlaid on the preceding ordination (Fig. 35), the meroplanktonic fish eggs, tornaria and brachyuran zoeae of

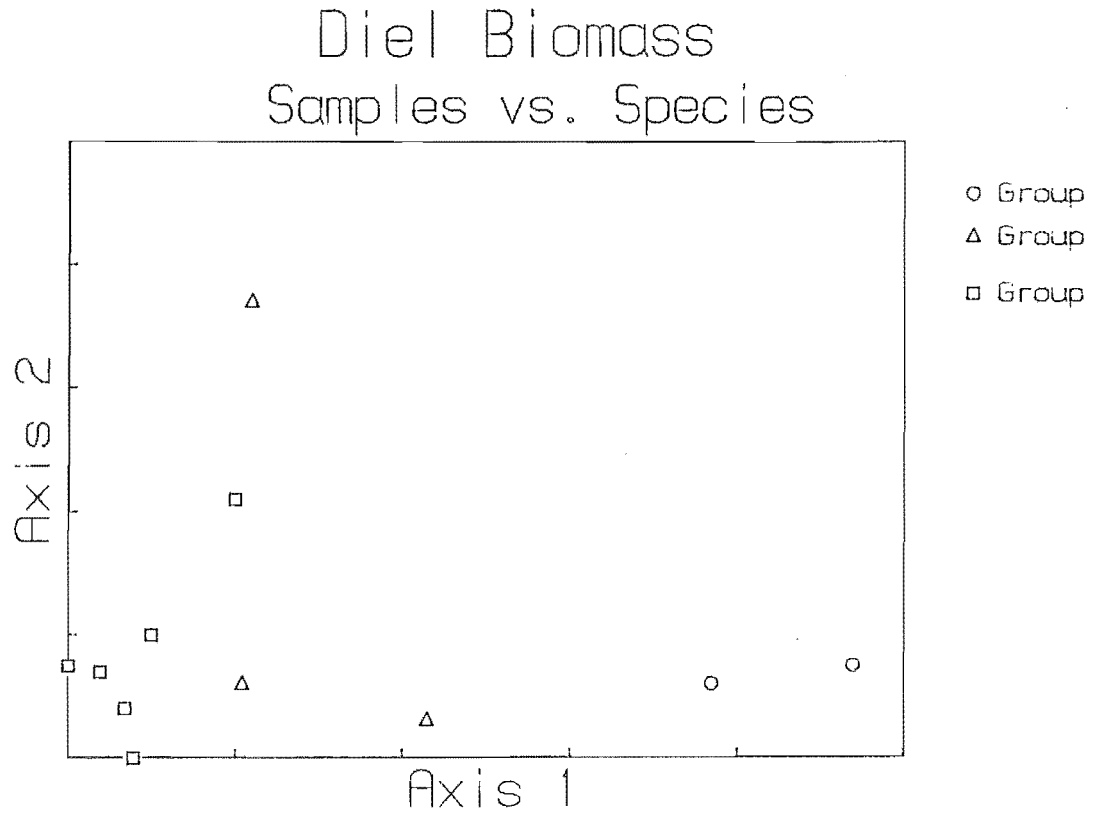


Fig. 35 Bray-Curtis ordination of total biomass in each diel sample in Brooklands Lagoon.

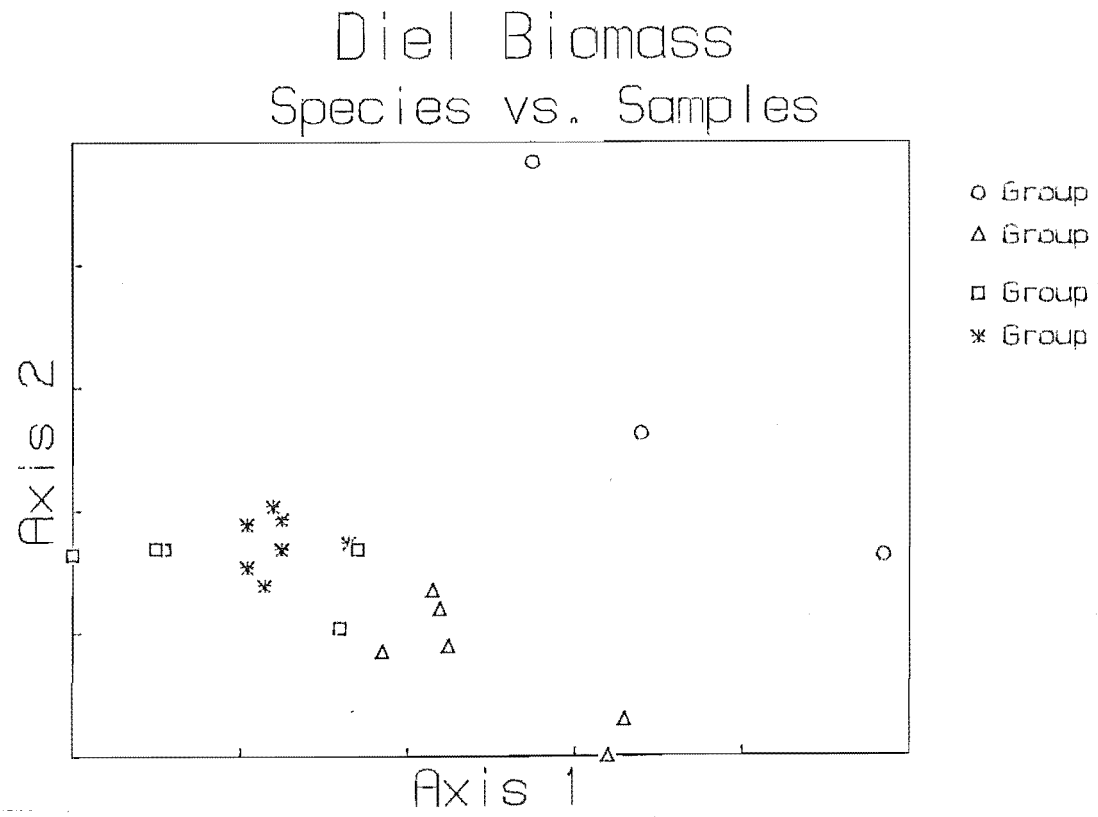


Fig. 36 Bray-Curtis ordination of taxa biomass from all diel samples in Brooklands Lagoon.

group 1 fell in early morning regions. They also occupy areas of high chlorophyll a concentration, high salinity and low temperatures in ordination space.

The second zooplankton cluster falls in a region of average turbidity and light period, but low salinity and low chlorophyll a concentrations. The copepods and freshwater species clusters (groups 3 & 4) plot on the lower left in sample ordination space. This region correlated with high chlorophyll a concentrations, high salinity and dark evening periods with high turbidity readings.

DISCUSSION

Seasonal Pattern

The faunal groups representing the largest proportion of biomass in Brooklands Lagoon were barnacle nauplii and fish eggs. These taxa occurred mainly in autumn and spring. An overall decrease in total zooplankton biomass, mainly due to decreased numbers of zooplankton, corresponded with greater diversity during July. Cyprids followed each burst of barnacle nauplii. However cyprids never represented as much biomass as the previous burst of nauplii. Tornaria, bivalve and gastropod veligers increased the biomass diversity when total biomass was low. Site one differed from the other two sites as it had far less biomass input from marine sources. At the estuary sites two and three, barnacle nauplii represented more biomass than copepod nauplii during summer, but meroplankton comprised less biomass than holoplankton fauna. In the spring copepods represented the most biomass during October and November. After this *Paratya curvirostris* and *Tenagomysis* sp. had higher biomass than the copepods during December.

The meroplankton were a large component of the biomass within the estuarine system of Brooklands Lagoon. This appears to contradict evidence provided by many other marine studies (see Raymont 1983 for review, Knox 1987). However most other studies have used coarser nets when sampling the macro-plankton and often omit the meroplankton because they are too difficult to work with (Deevey 1960a). The meroplankton is rarely separated and examined as a distinct component from the holoplankton. More usually these groups are combined for a total zooplankton biomass estimate.

The spring period of increasing warmth and plentiful food supply is a time for opportunistic species to rapidly increase population size (Knox 1987). This stage was first recognized in Brooklands Lagoon by increases in the phytoplankton production during September and October. This was followed by a succession of abundant holoplankton species similar to many other studies (Bougis 1976, Newell and Newell 1973, Colebrook 1964, Cameron and Pritchard 1963, Hardy 1970). During the short favourable growth period in November, December and January, *Acartia* sp., *M. heretunga* and *Microcyclops* sp. adults comprised the main biomass.

Autumn and early winter were the larval production season, when species prepared for the coming winter by increasing glycogen stores (Jillett 1968). This process is best carried out in the larval stages and results in an increased proportion of larval population representatives (Raymont 1983, Bougis 1976, Jillett 1968). Half of the year, from February through to August, had biomass comprising mostly copepod and barnacle nauplii, and tornaria larvae at site one (Fig. 26). Because the zooplankton comprised mainly meroplankton at this time, it suggests that the estuary is a harsh environment (Mclusky 1981, Knox 1987).

Meroplankton represented less biomass at the top of the estuary than at sites near the mouth. Biomass was represented by freshwater species such as *Camptocercus* sp., *Paratya curvirostris* and *Microcyclops* sp. during spring while the Waimakariri River flow was highest. A residential harpacticoid copepod, *Miscegenus heretunga*, dominated zooplankton biomass during the warmest month (January) while Waimakariri River flow was lowest.

Abrupt changes in composition of the biomass occur monthly in Brooklands Lagoon. However clear seasonal, successional changes could be separated from the data. Ordination of species biomass from all the samples showed that flood frequency combined with tidal volume were the main causes of variation. Tidal volume correlation explained the presence of several euryhaline marine species in group 4 (Fig. 29), *Paracalanus indicus, Euterpina acutifrons* and *Acartia* sp. Other species in this group are euryhaline estuarine taxa. For example, tornaria larvae, *M. heretunga*, bivalve veligers and barnacle and copepod nauplii. The presence of these species combined with the more euryhaline marine species can be explained by the positioning of the cluster in ordination space indicating a tolerance for higher flooding frequencies. Marine species can escape these events by not entering the estuary while meiobenthic species are able to shelter from adverse conditions by burrowing in the benthos (Hicks and Coull 1983, Riley 1967). Larger species in ordination group 1 occupy space correlating with low tide periods and medium flood frequencies. These less euryhaline species are more able to maintain position in the required water column by swimming (Bougis 1976), so do not appear in samples until low tide. The freshwater species clumped together in ordination space correlating with lowest flood frequency and Waimakariri River flow.

Meroplankters of group 3 cluster overlapped group 4, which represented euryhaline holoplankton. This position suggests that the larvae of benthic species are tolerant of a wide salinity range and therefore a more resistant stage in the life history (Jillett 1968, Raymont 1983).

Changes in meroplankton were as important in estimating total biomass within Brooklands Lagoon as those in the holoplankton. This effect was in direct contrast to many other studies (see Raymont 1983 for review). During the winter barnacle and copepod nauplii comprised up to 50% of the biomass. When these groups decreased in proportion veligers and cyprids increased (Fig. 32).

Biomass comparisons were made with the nearby Avon-Heathcote estuary zooplankton fauna recorded by Roper et. al. (1983), using species densities treated with my own dry weight conversion factors. Conversions from abundances per cubic metre were made for ten taxa common to both surveys from March to August. These species were, barnacle and copepod nauplii, barnacle cyprids, tornaria larvae, gastropod and bivalve veligers, *Paracalanus indicus*, *Oithona similis*, *Euterpina acutifrons* and *Centropages aucklandicus*.

Compared with the Avon-Heathcote estuary, total biomass in Brooklands Lagoon was at least nine to ten times less in all months (Fig. 37). Autumn increases in biomass occurred at both locations during April and May. However for the Avon-Heathcote estuary the biomass exhibited a three fold increase in August. Such an increase did not occur in Brooklands Lagoon; however in August Waimakariri River flow was highest and had the greatest number of floods.

The Avon-Heathcote is not subjected to large volumes of freshwater runoff flow and has longer retention than Brooklands Lagoon (Knox and Bolton 1977, Knox and Kilner 1973). The Avon-Heathcote estuary has an average

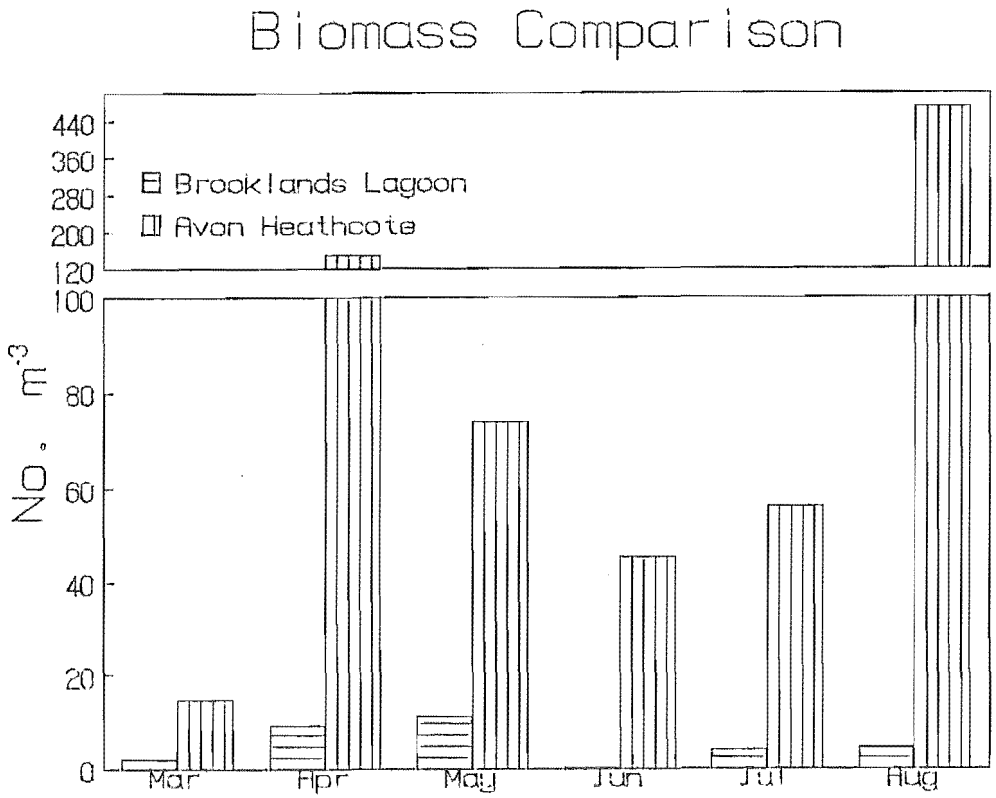


Fig. 37 Biomass totals compared between Brooklands Lagoon and Avon-Heathcote estuary for March to August. (Data converted from Roper et. al. 1982).

freshwater flow of 155 cumecs (Knox & Kilner 1973) compared to an average flow past the mouth of Brooklands Lagoon of 1250 cumecs in 1986 (Christchurch Drainage Board Records). Longer water retention and lower freshwater flow allow plankton to survive undisturbed, allowing a higher diversity (Knox 1987). Seasonal fluctuations in biomass within Brooklands Lagoon may be overshadowed by changes in river flow.

DIEL PATTERN

Cluster analysis showed that samples from the diel survey were more similar than those collected during the seasonal survey. The longest relative distance separating diel clusters was 1.09 compared with seasonal cluster distances which exceeded 2.8. This could be expected because of the short time between each sample.

Ordination of diel biomass data has shown that brachyuran zoeae, tornaria and fish eggs prefer the brightest conditions. These fauna are very weak swimmers and less able to avoid strong currents or seek shelter. As larval phases of benthic species often have a dispersal function (Davis 1955, Bougis 1976), they could be expected to be attracted to light. At the water surface these taxa would be subject to the strongest currents for distribution (Mclusky 1981, Hardy 1956)

The remaining groups from cluster analysis consisted almost entirely of holoplankton and fell in early morning and high turbidity space. At this time of day, light was weakest supporting the theory that zooplankton migrate toward the surface during the night (Ewald 1912). In this ordination space chlorophyll a concentrations were lower, but reduced visibility to predators in dark conditions (Hardy 1956) would let these species feed longer undisturbed.

The importance of water turbidity as shown in the present study contradicts the findings of Roper et. al. (1983) who suggested that water turbidity had no effect on distribution within estuaries. Unfortunately there are no records of distribution of zooplankton through the water column within the lagoon because of the shallow depth. Therefore zooplankton patterns may be due to tidal appearance of meiobenthic species.

CONCLUSIONS

The biomass in Brooklands Lagoon depends greatly on river flow which may disguise seasonal events. River flow may not only reduce zooplankton production and biomass, but also restricts the entry of species into the estuary. Because river flow changes less in a day, biological and environmental variables may affect zooplankton biomass. There is a strong pattern of diurnal migration away from light by the holoplankton which are able to retreat to deeper coastal water at low tide or shelter in the benthos during adverse conditions. The estuary has very little biomass represented by resident species and diurnal migrations are made daily by coastal species if river flow permits. Coastal species entering this environment are those able to tolerate physico-chemical extremes, possibly to avoid predation, or make use of an alternative food supply, or both.

CHAPTER FIVE

LABORATORY INVESTIGATIONS OF PLANKTON AND PREDATORY FISHES

INTRODUCTION

Brooklands lagoon acts as a nursery area for larval flatfish, where the shallow tidal flats provide food and shelter from predation. The lagoon has become quite important to the local fishing industry, which has a flatfish catch comprising mostly yellow bellied flounder, *Rhombosolea leporina* and *R. plebia*. These species live in Pegasus Bay using estuaries and shallow water embayments along the Canterbury coast to spawn and support the early stages of their life history (Mundy 1963, Roper 1979). Although a great deal of research has shown the importance of zooplankton in the diet of larval and juvenile fishes in the northern hemisphere there is very little comparable research in New Zealand (Hardy 1970, Hicks and Coull 1983 for reviews). Intensive predation by higher trophic levels such as the larval fish could have an effect on zooplankton populations in Brooklands Lagoon.

As well as being affected by predation zooplankton are also affected by environmental variables. Preferences and tolerances of individual physico-chemical factors differs between species (Odum 1971, Hardy 1970, Bougis 1976). Each environmental factor may act as a grading mechanism to control species distribution. For example, in copepods temperature affects the development rate (Davis 1984), feeding rate (Conover 1964) and the reproductive rate (Hicks and Coull 1983). Temperature and salinty are the primary factors controlling many zooplankton distribution patterns (Bougis 1976). *Miscegenus heretunga*, a common harpacticoid copepod, was chosen for laboratory experiments to investigate salinity and temperature responses. This species, which forms part of the diet of juvenile

fishes , survived well in the laboratory. Salinity and temperature tolerances were investigated for temperatures between 5-25°C and salinities between 5-100% seawater.

METHODS

During the seasonal survey, fyke traps were set (using bread bait) to catch very small juvenile stages of *Mugil cephalus*, while hand trawls were made for *Rhombosolea plebia*. These species were the planktivorous fish in Brooklands Lagoon recorded by Knox and Bolton (1977). The specimens were killed and preserved in 10% formalin and were dissected in the laboratory for gut content determinations.

Miscegenus heretunga were collected in Zooplankton trawls using the same equipment described earlier. Specimens were kept alive in thermos flasks for transport to the laboratory and kept at room temperature in an aerated 20 litre aquarium with a fine gravel sediment. Water used was seawater diluted with a ratio of 4:1 with filtered estuary water.

Ten individuals were placed in 200 ml. crystalizing dishes with 100 ml. of filtered, sterilized seawater, for 24 hours in a 12:12 hour photoperiod. Three replicate experiments were established with salinity concentrations of 5%, 50% and 100% from seawater of 34 ppt. salinity. The dishes were placed in temperatures of 5°C, 10°C, 20°C and 25°C. The control experiment was 10°C and 5% seawater, which were the conditions within Brooklands Lagoon at the time of collection. Each dish was checked at intervals of 0.1, 0.5, 1, 2, 4, 8, 16 and 24 hours and dead animals were removed to prevent fouling. Survival data were used to construct surface response curves.

RESULTS

Fish Diet

Mugil cephalus, the yellow eyed mullet found in Brooklands Lagoon, fed on a variety of food material (Fig. 38). However fish from 120-160mm length exhibited a marked preference for a zooplankton diet. The smallest mullet (100-120mm.) fed mainly on oligochaetes. The middle size range of the mullet (120-140mm.) sampled fed almost exclusively on cyclopoid copepods, a faster swimming prey than ostracods or oligochaetes. Some larger *Daphnia carinata*, another free swimming zooplankter, were also found in the gut contents of these fish. The largest size class of *M. cephalus* contained a much larger mass of oligochaetes and a few copepods. Overall ten classes of prey were found in the stomachs of *M. cephalus*, these were; cyclopoid copepods, calanoid copepods, *Daphnia carinata*, gastropod veligers, isopods, barnacle cyprids, oligochaetes, ostracods, mysids and crab megalopae. Larger prey such as the mysids and megalopae comprised less than 1% of the stomach contents.

For the Sand flounder, *Rhombosolea plebia*, prey size increased with fish size (Fig. 38). The smallest fish (10-20mm.) length, were consuming harpacticoid copepods almost exclusively, however isopods and other zooplankton were included in their diet. The middle size range sampled (20-30mm.) were also eating mainly harpacticoids, but showed a preference for isopods and other zooplankton. The largest size flounders, 30-50mm ate crab megalopae only. Harpacticoid copepods formed 91.2% of the stomach contents of *R. plebia* and of these 98.5% were *M. heretunga*. Altogether seven prey types were found in the stomachs of *R. plebia*: harpacticoid copepods, *Daphnia carinata*, isopods, tornaria, copepod nauplii and crab megalopae. 15 *R. plebia* and 18 *M. cephalus* caught during the flood tide had empty stomachs.

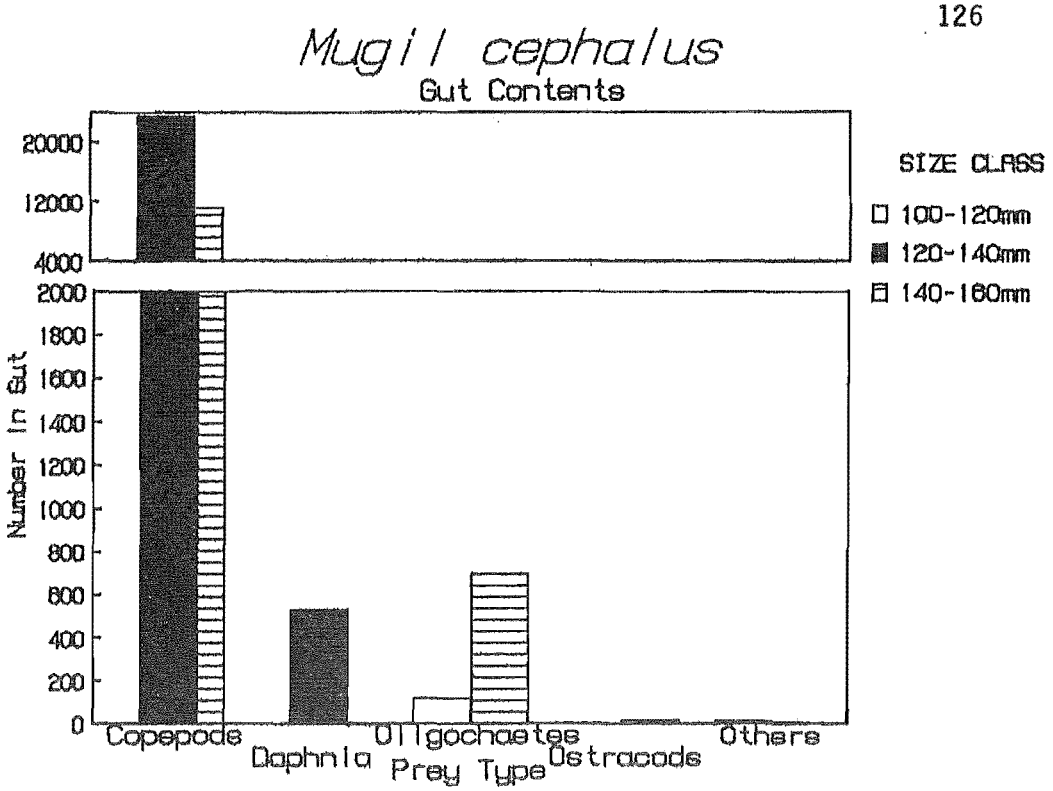


Fig. 38 Diet analysis of larval *Mugil cephalus* taken from Brooklands Lagoon during February 1986.

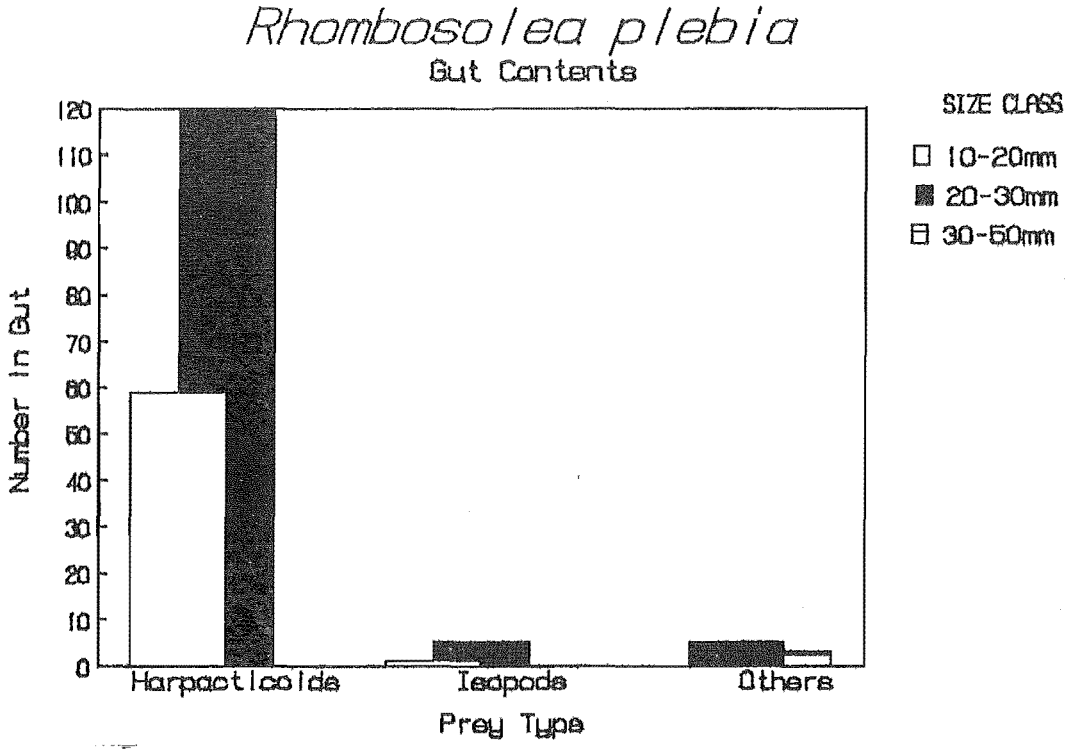


Fig. 39 Diet analysis of larval *Rhombosolea plebia* taken from Brooklands Lagoon during February 1986.

Salinity and Temperature Response of *Miscegenus heretunga*.

Survival data from 24 hour salinity and temperature tolerance experiments were used to construct response curves for *Miscegenus heretunga* (Fig. 40). Percentage survival estimates for *M. heretunga* show a wide temperature/ salinity tolerance. *M. heretunga* is able to survive between 0-27°C and in the salinity range 2 ppt. to more than 40ppt. These limits have been extrapolated from experimental reults (Fig. 40). The animals did not survive in temperatures less than 5°C when combined with salinities lower than 4ppt. In the higher temperature range, temperatures above 27°C could not be tolerated at any salinity. 100% salinity was tolerated at temperatures below 10°C. The preferred salinity/ temperature range shown by 55% of the population was in temperatures of less than 5°C to 25°C and in salinities bewteen 6 ppt. to 34 ppt.A noticable skew was apparent in the reponse surface of 55% survival range. This increased the preferred salinity range at lower temperatures. Optimal conditions with 100% survival occurred at 15°C and 17ppt salinity.

DISCUSSION

Although studies by Mundy (1963), Roper (1979) and Livingston (1987) recorded the diet of adult *R. plebia* they did not record the diet of larval fish and zooplankton was not recorded in the diet. Many small larval fish are dependent on plankton as part of their early dietary requirements (Hardy 1956, Hicks and Coull 1983). Larval *Rhombosolea plebia* and *Mugil cephalus* were shown in this study to be feeding on the zooplankton, but using different species of plankton as their major dietary component. This suggests that there is little competition for food between them and little resource overlap. *M.*

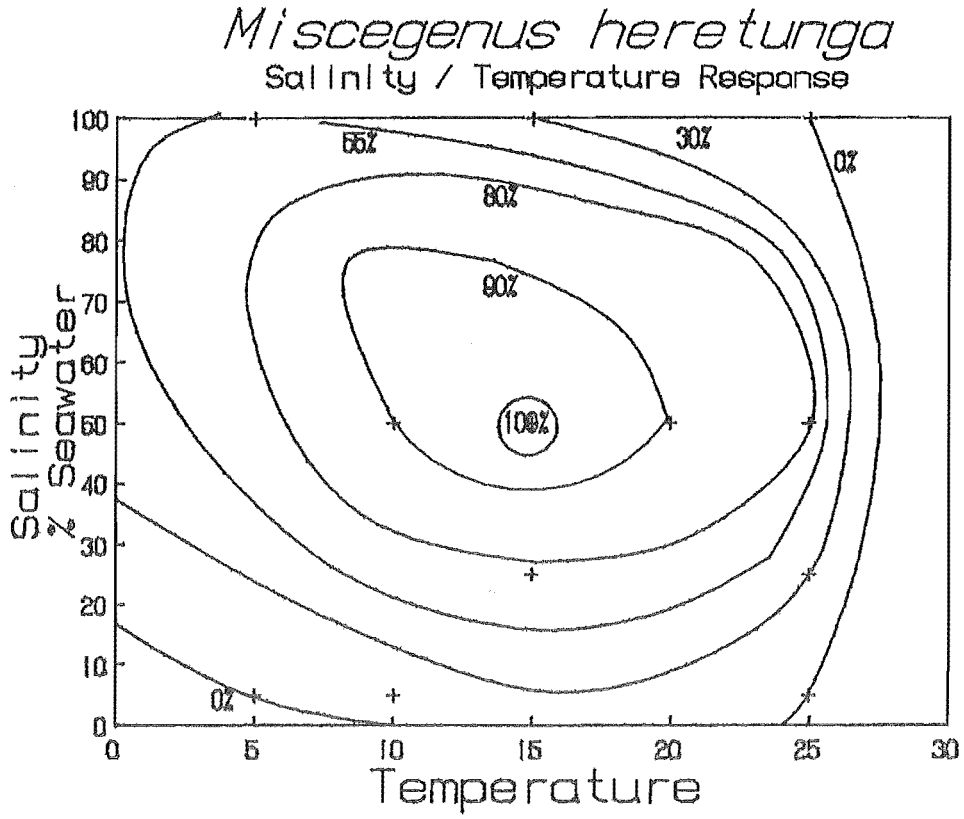


Fig. 40 Salinity, temperature response surface for *Miscegenus heretunga* following 24 hours survival measures.

cephalus appears to have less specific prey species requirements, feeding on oligochaetes at smallest and largest size classes sampled, while *R. plebia* was more specific in its dietary requirements.

Reliance by *R. plebia* on a single species as a major diet component indicates an important role for *Miscegenus heretunga* as a lower food web species within the estuary. *M. heretunga* must therefore be present in sufficient numbers throughout the year to renew its own population and support *R. plebia*. However behavioural mechanisms of *M.heretunga* may allow it to escape predation pressure by burrowing in the bottom sediment at low tide (Hicks and Coull 1983). Planktivorous fishes were shown not to feed during this period and may have been seeking shelter themselves. These fish may be resting on the bottom in the case of *R. plebia*, or retreat to the sea in the case of *M. cephalus*. On the flood tide feeding most likely resumes as prey move out of the benthos into the water column.

Mundy (1963), Livingston (1987) and Roper (1979) showed that flatfishes switch to larger prey as they grow. The same feature was seen in the larval flatfish population of Brooklands Lagoon, which switched from small harpacticoids and isopods to crab megalopae as they grew. This behaviour pattern of the flatfish (Roper 1979) may reduce predation on the population of *M. heretunga* allowing them to recover. Many previous workers have emphasized that the estuary is an important stage in the development and nurturing of larval flatfishes before they move to the sea (Roper 1979, Mundy 1963). The current study supports others in demonstrationg the importance of harpacticoid copepods as a major diet component of flatfish (see Hicks and Coull 1983 for review).

Previous studies in the South Island of New Zealand have assumed that smaller flatfish were absent from the estuarine environment and they placed the earliest life history stages of these fish as non-feeding, migratory phases (Mundy 1963). These were assumed to migrate from the spawning grounds in coastal waters to the nursery areas. This survey suggests that flatfish eggs may be hatched in shallow, tidal waters and the larvae feed there before moving seaward.

The harpacticoid *Miscegenus heretunga* has been recorded as a euryhaline, meiobenthic species, based on taxonomic similarities to other harpacticoids from similar environments (Hicks 1982). *Euterpina acutifrons* a common temperate harpacticoid copepod from New Zealand coastal waters (Moreira et. al. 1982) was shown to tolerate temperatures from <5-24°C and salinities from 10-65ppt. Although the overall temperature tolerance range was the same, *M. heretunga* was able to tolerate much lower salinities. This result is in keeping with the known distribution of this species from diluted, intertidal meiobenthos. *E. acutifrons* is a neritic, harpacticoid from temperate waters and a common representative of marine waters within estuaries (see Knox 1987 for review). This species would is not normally exposed to dilute environments for long periods, and unable to survive if trapped there for any length of time.

M. heretunga may have behavioural responses for avoiding extreme temperature conditions. Such behaviours have been recorded within the harpacticoid copepods before (see Hicks and Coull 1983 for review) and include burrowing into the sediment to a more suitable microhabitat.

The tolerance range of many invertebrates is greater than the environments in which they are found (Newell 1976). The tolerance range exhibited by *M. heretunga* is close to its habitat and is less

than that which would be expected in the summer. Some species modify temperature tolerance seasonally and others may have behaviour patterns for avoiding potentially lethal conditions. Such behaviour has been recorded for harpacticoid copepods (see Hicks and Coull 1983 for review) and it is likely that burrowing by *M. heretunga* provides a habitat of reduced temperature and favourable salinities.

CHAPTER SIX

DISCUSSION AND CONCLUSIONS

Because of either frequent environmental disturbance such as floods, or extreme conditions such as very cold river flow. Brooklands Lagoon estuary has a very depauperate fauna. Compared with many other studies, the number of zooplankton species within Brooklands Lagoon is a half to a third of the number of species normally found in New Zealand coastal and estuarine waters (Jillett 1969, Bradford 1972, Roper et. al. 1983) and about one fifth of those recorded in the northern hemisphere estuaries. The adjacent Avon-Heathcote estuary, which is less affected by freshwater flow than Brooklands Lagoon, has only approximately half the number of species present in northern hemisphere estuaries.

Although the Brooklands Lagoon taxa list includes a diverse range of species many are very rare and cannot be used as indicators. However species such as *Euterpina acutifrons* and *Paracalanus indicus* indicate that marine waters entering the estuary (Jeffries 1962a) are influenced by temperate and colder sub-antarctic water masses respectively. Only zooplankton species found in shallow coastal waters enter the estuary as the absence of deeper water chaetognaths and larger copepods testifies.

Ordination supports the view that zooplankton are good indicators of environmental conditions within the estuary (Jeffries 1962a). These analyses have highlighted *Microcyclops* sp. and *Paratya curvirostris* as indicators of freshwater flow, *Acartia* sp. an indicator of neritic waters and *Miscegenus heretunga* indicating resident estuarine environmental conditions.

Analysis of the zooplankton community using biomass conversions showed that those species with the highest densities also had the greatest biomass. Few exceptions were found, however the less

numerous brachyuran zoeae represented a significant amount of biomass in the upper estuary and *Paracalanus indicus* represented a larger amount of biomass at the mouth of the estuary. Despite slight variations from site to site and large fluctuations from month to month, several species were constantly dominant in both analyses. These species were *Acartia* sp., *Miscegenus heretunga*, *Paratya curvirostris*, *Microcyclops* sp. and *Camptocercus* sp.

The most important species from both biomass and numerical analyses highlight the same environmental factors causing zooplankton fluctuations. Numerical analyses indicated salinity was the primary cause of zooplankton abundance changes, while biomass estimates indicated tidal volume and flood frequency were the primary causes. All of these variables are associated with hydrological variation within Brooklands Lagoon notably Waimakariri River flow. River flow acts as a gate to the estuary ecosystem, allowing the marine waters to mix during high tide or low flow periods.

The most important species shown by ordination to indicate environmental conditions within Brooklands Lagoon were the freshwater holoplankton, including the copepod *Microcyclops* sp., *Camptocercus* sp., and also *Acartia* sp. Meroplankton that formed significant proportions of either numbers or biomass were fish eggs and barnacle and copepod nauplii. Brachyuran zoeae were shown to comprise a significant amount of the biomass furthest from the sea, in waters comprising well mixed river and sea water. In all cases these animals tended to represent rapidly fluctuating, transient stages in the ordination analyses. They also had lower, less reliable correlation coefficients with each axis.

Secondary variation within Brooklands Lagoon was also attributed to similar causes by both numerical and biomass analyses. Abundance analysis suggested that season was of secondary importance ($r=0.200$),

while biomass ordination suggested temperature (r=-0.567) was of secondary importance. Because temperature was shown to fluctuate in a regular annual cycle, it indirectly confirms seasonality as an important environmental variable in Brooklands Lagoon.

Just as the seasonal survey showed similar results between numerical and biomass analyses, so too did diel analyses. However biomass data served to reduce species diversity of the representative taxa and exhibited the best correlation coefficients linking environmental factors with zooplankton biomass. Both analyses highlighted the same environmental variables as possible causes of zooplankton distribution patterns. The primary variable separated was water turbidity on axis one of the ordinations (r=0.487). Diel period was a secondarily selected variable showing good correlation with axis two (r=-0.584). These two factors probably act together to affect light intensity thereby influencing zooplankton behaviour (Ewald 1912).

When separate species biomasses were correlated with the ordination axes the best matches were obtained for freshwater species and copepods. These species had the greatest individual biomass and would be the most visible to predators (Davis 1955, Newell and Newell 1973, Bougis 1976). This implies that these species are using conditions within the estuary to their advantage. One disadvantage for these grazing species however must be reduced chlorophyll a concentrations within the estuary. Chlorophyll a concentration correlated strongly as a secondary factor affecting zooplankton distribution.

Results from the diel ordination suggest that the species within Brooklands Lagoon may have actively moved into this environment. Hardy (1956) and Jeffries (1962) suggest that marine species may be there to utilise an otherwise unused food source. Alternatively the

marine species may have moved into the estuary to escape predation pressure from marine hunters. They may be hiding in turbid estuary waters as the current study shows, or moving into a physiologically limiting habitat for predators (Riley 1967).

Estuaries are characterised as rich and productive environments supporting a large biomass with rapid turnover times (Knox 1987). However relatively few species have adapted to the rapid changes that occur continually within estuaries (Mclusky 1981). The hydrological characteristics of estuaries cause these environments to self destruct within a short time, by filling with sediments carried by terrestrial runoff (Heath 1985). Because of the low stability and high production rates of organisms living in the estuarine habitat, Sanders (1969) developed the stability-time hypothesis for comparison of this habitat with other marine benthos.

This study has shown the major causes of variation within the zooplankton population of Brooklands Lagoon is caused mainly by river flow and photoperiod. These conditions may fluctuate widely in an unpredictable manner and Sanders (1969) has described the estuary as a 'physically controlled community'. Animals in the zooplankton of estuaries must therefore be tolerant of severe physiological stress. To overcome frequent stress factors, zooplankton may be r-selected, with high reproduction rates. Sucha life history strategy is shown by *Pseudocalanus* sp. (Davis 1984), a calanoid copepod related to *Acartia* sp. found in Brooklands Lagoon. *Acartia* sp. is an opportunistic species and the first to appear in the spring zooplankton blooms. Here they take advantage of warmer conditions and more abundant food supplies. Opportunistic species may also occur in large numbers at other times of the year, taking advantage of unseasonally warm local conditions to reproduce (Odum 1971).

Another adaption of zooplankton to the estuarine environment is tolerance of rapid changes. Zooplankton of estuaries are often have wide tolerance ranges for many factors and are often able to tolerate conditons beyond those normally experienced in estuaries (Knox 1987). *Miscegenus heretunga* was found to be able to tolerate a wide range of salinities from less than 5 ppt. to over 34 ppt. for 24 hours. These characteristics would enable it to survive freshwater floods from terrestial runoff or alternatively, high salinities during low tide caused by evaporation. Although not able to withstand a wide range of temperatures in the laboratory (<5-27°C), behavioural adaptation allows this species to escape temperature extremes by burrowing in the benthos to find a more insulated micro-environment (Hicks 1971, Hicks & Coull 1983). Clearly the distribution pattern of zooplankton in Brooklands Lagoon depends upon a complex of interactions; the harsh environment, the life history strategies and physiological and behavioural adaptations of the organisms.

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APPENDIX A: Seasonal survey, species abundances per litre.

SITE/ MONTH	DEC-85	JAN	FEB	MAR	APR	MAY	JUN	JUL	AUG	SEP	OCT	NOV	DEC86
Barnacle nauplii	.00	1032.00	2.67	29.33	5.33	12.00	.00	12.00	30.67	.00	.00	9.33	.00
Copepod Nauplii	109.33	205.33	.00	40.00	108.00	518.67	4.00	518.67	558.67	21.33	8.00	22.67	9.33
Barnacle Cyprids	.00	26.67	.00	4.00	2.67	6.67	10.67	6.67	.00	17.33	4.00	8.00	2.67
Anomuran Zoae	.00	.00	.00	.00	.00	.00	.00	.00	1.33	.00	.00	.00	.00
Brachyuran Zoae	8.00	14.67	.00	.00	.00	1.33	.00	1.33	.00	.00	.00	1.33	.00
Tornaria	20.00	30.67	10.67	13.33	5.33	12.00	1.33	12.00	153.33	8.00	.00	12.00	5.33
Phoronid Larvae	1.33	.00	.00	.00	.00	.00	.00	.00	.00	.00	1.33	.00	.00
Gastropod veligers	66.67	.00	24.00	.00	.00	.00	13.33	.00	6.67	8.00	.00	.00	150.67
Bivalve Veligers	.00	2536.00	.00	285.33	37.33	10.67	.00	10.67	6.67	2.67	2.67	2.67	.00
Pluteus larvae	.00	4.00	.00	17.33	.00	.00	.00	.00	2.67	.00	.00	10.67	2.67
Mysidacea	.00	.00	.00	1.33	.00	18.67	.00	18.67	.00	.00	.00	.00	.00
Cumacea	.00	.00	.00	.00	.00	.00	.00	.00	.00	.00	.00	.00	.00
Acartia sp.	169.33	373.33	.00	12.00	5.33	22.67	1.33	22.67	144.00	1.33	.00	.00	.00
Paracalanus indicus	.00	2.67	.00	.00	10.67	.00	1.33	.00	128.00	.00	.00	1.33	.00
Oithona sp.	21.33	1.33	.00	.00	.00	24.00	1.33	24.00	57.33	.00	.00	2.67	.00
Microcyclops sp.	.00	.00	.00	85.33	14.67	8.00	9.33	8.00	25.33	60.00	24.00	22.67	12.00
Temora turbinata	.00	2.67	14.67	5.33	.00	8.00	5.33	8.00	.00	.00	.00	.00	.00
Centropages aucklandicus	.00	1.33	.00	.00	.00	1.33	.00	1.33	.00	.00	.00	.00	.00
Gladioferans pectinatus	.00	.00	.00	.00	.00	.00	.00	.00	1.33	.00	.00	.00	.00
Euterpina acutifrons	.00	5.33	.00	4.00	24.00	10.67	.00	10.67	6.67	.00	.00	.00	.00
M. heretunga F	258.67	265.33	9.33	142.67	69.33	12.00	6.67	12.00	10.67	8.00	5.33	62.67	213.33
M. heretunga M	.00	.00	.00	.00	.00	6.67	.00	6.67	.00	4.00	5.33	8.00	96.00
Harpacticus sp.	.00	5.33	.00	12.00	.00	.00	.00	.00	.00	.00	.00	.00	.00
Sharknose harpacticoid	.00	4.00	.00	.00	.00	1.33	.00	1.33	.00	.00	.00	.00	.00
Scutellidium sp.	.00	.00	.00	4.00	13.33	1.33	.00	1.33	.00	1.33	4.00	.00	6.67
Ostracoda	.00	1.33	.00	2.67	5.33	.00	.00	.00	.00	.00	1.33	5.33	.00
Daphnia carinata	24.00	1.33	.00	.00	5.33	13.33	.00	13.33	32.00	6.67	5.33	.00	.00
Simocephalus vetulius	1.33	.00	.00	.00	.00	.00	.00	.00	5.33	.00	.00	4.00	.00
Camptocercus sp.	5.33	.00	.00	.00	.00	.00	.00	.00	8.00	10.67	16.00	42.00	20.00
Quinquelaophonte sp.	1.33	.00	34.67	.00	.00	4.00	.00	4.00	2.67	1.33	1.33	.00	2.67
Halectinosoma sp.	.00	.00	.00	.00	.00	.00	.00	.00	1.33	1.33	.00	.00	1.33
Isopoda	.00	.00	.00	.00	.00	.00	.00	.00	.00	.00	.00	1.33	.00
Paratya curvirostris	56.00	22.67	1.33	5.33	1.33	.00	.00	.00	.00	.00	8.00	48.00	41.33
Cryptoniscidae	.00	9.33	1.33	.00	.00	5.33	.00	5.33	.00	.00	.00	.00	.00
Amphipoda	.00	.00	.00	.00	.00	.00	.00	.00	.00	.00	.00	.00	.00
Ctenophora	.00	.00	.00	.00	.00	.00	.00	.00	.00	2.67	.00	1.33	.00
Hydromedusae	.00	.00	.00	.00	.00	1.33	.00	1.33	.00	.00	.00	.00	.00
Anthomedusae	.00	.00	9.33	.00	.00	.00	.00	.00	.00	.00	.00	.00	.00
Scyphomedusae	.00	.00	.00	.00	.00	.00	.00	.00	.00	.00	.00	.00	.00
Radiolaria	.00	5.33	.00	.00	2.67	1.33	1.33	1.33	.00	.00	.00	.00	.00
Ascidacea	.00	.00	.00	6.67	.00	8.00	.00	8.00	.00	.00	.00	.00	.00
Fish larvae	.00	22.67	1.33	2.67	.00	2.67	1.33	2.67	.00	8.00	.00	2.67	9.33
Fish Eggs	4.00	97.33	462.67	85.33	68.00	149.33	1.33	149.33	1.33	.00	1.33	5.33	.00

APPENDIX B: Seasonal survey, species abundances per litre.

SITE 2\ MONTH	DEC-85	JAN	FEB	MAR	APR	MAY	JUN	JUL	AUG	SEP	OCT	NOV	DEC86
Barnacle nauplii	.00	23278.67	97.33	756.00	3132.00	1025.33	12.00	1013.33	486.67	18.67	52.00	10.67	29.33
Copepod Nauplii	13618.67	3376.00	28.00	101.33	1066.67	632.00	6.67	512.00	870.67	28.00	162.67	24.00	5.33
Barnacle Cyprids	70.67	113.33	8.00	8.00	5.33	221.33	5.33	48.00	4.00	752.00	9.33	10.67	10.67
Anomuran Zoae	.00	12.00	.00	.00	.00	.00	.00	.00	.00	.00	.00	.00	.00
Brachyuran Zoae	324.00	92.00	20.00	20.00	.00	.00	.00	.00	1.33	.00	1.33	.00	4.00
Tornaria	102.67	402.67	34.67	73.33	65.33	90.67	.00	14.67	176.00	5.33	2.67	28.00	202.67
Phoronid Larvae	.00	.00	.00	.00	.00	.00	.00	.00	.00	.00	.00	.00	.00
Gastropod veligers	146.67	.00	306.67	.00	.00	246.67	4.00	229.33	10.67	5.33	28.00	9.33	132.00
Bivalve Veligers	.00	965.33	.00	66.67	98.67	1610.67	.00	90.67	72.00	2.67	4.00	6.67	.00
Pluteus larvae	1.33	.00	.00	4.00	.00	2.67	.00	1.33	.00	.00	.00	.00	1.33
Mysidacea	10.67	16.00	.00	1.33	.00	21.33	.00	33.33	.00	.00	.00	.00	.00
Cumacea	.00	.00	.00	.00	.00	1.33	.00	1.33	1.33	.00	.00	.00	.00
Acartia sp.	889.33	11569.33	168.00	16.00	20.00	268.00	1.33	114.67	866.67	9.33	10.67	6.67	.00
Paracalanus indicus	12.00	2424.00	.00	.00	86.67	80.00	.00	12.00	486.67	1.33	33.33	8.00	2.67
Oithona sp.	1.33	9.33	.00	.00	.00	40.00	.00	34.67	53.33	1.33	1.33	5.33	.00
Microcyclops sp.	1.33	.00	.00	28.00	10.67	18.67	14.67	6.67	8.00	34.67	50.67	12.00	9.33
Temora turbinata	2.67	2.67	1.33	.00	.00	9.33	.00	8.00	.00	.00	.00	.00	.00
Centropages aucklandicus	.00	214.67	.00	.00	.00	49.33	.00	4.00	.00	1.33	.00	.00	.00
Gladioferans pectinatus	.00	.00	.00	.00	.00	.00	.00	.00	.00	.00	.00	.00	.00
Euterpina acutifrons	.00	22.67	.00	1.33	98.67	1525.33	.00	40.00	32.00	1.33	14.67	.00	.00
M. heretunga F	138.67	5232.00	626.67	185.33	120.00	17.33	17.33	12.00	4.00	120.00	13.33	37.33	34.67
M. heretunga M	.00	.00	.00	.00	.00	4.00	.00	8.00	6.67	42.67	5.33	14.67	36.00
Harpacticus sp.	2.67	42.67	.00	1.33	1.33	1.33	.00	.00	.00	.00	.00	.00	.00
Sharknose harpacticoid	1.33	9.33	.00	1.33	.00	.00	.00	.00	.00	.00	.00	.00	4.00
Scutellidium sp.	.00	.00	1.33	.00	1.33	2.67	1.33	4.00	1.33	1.33	8.00	2.67	4.00
Ostracoda	.00	52.00	.00	1.33	2.67	.00	.00	.00	.00	61.33	1.33	6.67	194.67
Daphnia carinata	2.67	.00	1.33	2.67	4.00	.00	8.00	5.33	9.33	8.00	1.33	.00	.00
Simocephalus vetulus	.00	.00	.00	.00	.00	.00	.00	.00	.00	.00	.00	.00	.00
Camptocercus sp.	1.33	.00	.00	.00	.00	.00	.00	.00	4.00	4.00	25.33	21.33	2.67
Quinquelaophonte sp.	5.33	.00	68.00	.00	.00	2.67	.00	2.67	1.33	4.00	2.67	2.67	4.00
Halectinosoma sp.	.00	.00	.00	.00	.00	.00	.00	1.33	1.33	.00	.00	.00	.00
Isopoda	1.33	.00	.00	.00	.00	.00	.00	.00	.00	2.67	.00	.00	.00
Paratya curvirostris	44.00	40.00	2.67	6.67	1.33	.00	.00	.00	.00	2.67	5.33	33.33	128.00
Cryptoniscidae	14.67	49.33	2.67	.00	2.67	.00	1.33	.00	.00	.00	1.33	.00	.00
Amphipoda	.00	.00	.00	.00	.00	.00	1.33	.00	.00	.00	.00	.00	.00
Ctenophora	.00	66.67	.00	.00	.00	1.33	.00	1.33	.00	.00	.00	.00	.00
Hydromedusae	.00	.00	.00	1.33	.00	9.33	.00	.00	.00	.00	.00	.00	.00
Anthomedusae	.00	1.33	.00	.00	1.33	.00	.00	1.33	1.33	.00	.00	.00	.00
Scyphomedusae	.00	.00	.00	.00	.00	.00	.00	.00	2.67	1.33	.00	.00	.00
Radiolaria	.00	198.67	.00	14.67	12.00	80.00	.00	8.00	.00	.00	.00	.00	.00
Ascidacea	.00	.00	.00	.00	.00	14.67	.00	9.33	.00	.00	.00	.00	.00
Fish larvae	2.67	14.67	2.67	.00	.00	1.33	.00	.00	.00	.00	1.33	.00	1.33
Fish Eggs	69.33	60.00	88.00	98.67	34.67	38.67	30.67	50.67	13.33	5.33	.00	4.00	.00

APPENDIX C: Seasonal survey, species abundances per litre

SITE 3\ MONTH	DEC-85	JAN	FEB	MAR	APR	MAY	JUN	JUL	AUG	SEP	OCT	NOV	DEC86
Barnacle nauplii	361.33	4704.00	18.67	68.00	177.33	333.33	2.67	369.33	534.67	20.00	146.67	.00	12.00
Copepod Nauplii	1148.00	882.67	8.00	4.00	34.67	757.33	10.67	1284.00	1288.00	30.67	41.33	12.00	8.00
Barnacle Cyprids	128.00	101.33	12.00	65.33	18.67	288.00	16.00	5.33	1.33	14.67	18.67	2.67	25.33
Anomuran Zoae	.00	1.33	.00	.00	.00	.00	.00	.00	.00	.00	.00	.00	.00
Brachyuran Zoae	1066.67	165.33	190.67	9.33	2.67	.00	.00	.00	.00	.00	.00	.00	.00
Tornaria	152.00	160.00	8.00	14.67	5.33	224.00	.00	24.00	325.33	6.67	22.67	10.67	149.33
Phoronid Larvae	.00	.00	.00	.00	.00	.00	.00	.00	.00	.00	.00	.00	.00
Gastropod veligers	428.00	.00	86.67	.00	.00	134.67	6.67	13.33	14.67	4.00	18.67	17.33	174.67
Bivalve Veligers	.00	473.33	.00	24.00	38.67	985.33	.00	24.00	126.67	12.00	8.00	5.33	1.33
Pluteus larvae	.00	.00	5.33	4.00	1.33	4.00	.00	4.00	1.33	.00	.00	2.67	1.33
Mysidacea	52.00	.00	.00	.00	.00	6.67	.00	9.33	.00	.00	.00	.00	.00
Cumacea	.00	.00	.00	.00	.00	.00	.00	.00	.00	.00	.00	.00	.00
Acartia sp.	1300.00	9390.67	101.33	9.33	8.00	284.00	5.33	454.67	1648.00	28.00	18.67	.00	2.67
Paracalanus indicus	.00	5.33	.00	.00	1.33	185.33	2.67	20.00	402.67	2.67	18.67	5.33	2.67
Oithona sp.	13.33	9.33	.00	.00	.00	40.00	.00	33.33	46.67	1.33	6.67	1.33	.00
Microcyclops sp.	.00	.00	.00	50.67	.00	24.00	20.00	6.67	16.00	33.33	126.67	9.33	24.00
Temora turbinata	5.33	1.33	.00	1.33	.00	6.67	.00	.00	.00	.00	.00	.00	.00
Centropages aucklandicus	6.67	8.00	.00	.00	.00	37.33	.00	1.33	.00	.00	.00	.00	.00
Gladioferans pectinatus	.00	.00	.00	.00	.00	.00	.00	.00	.00	.00	16.00	.00	4.00
Euterpina acutifrons	.00	.00	.00	.00	2.67	2214.67	.00	33.33	9.33	.00	28.00	.00	1.33
M. heretunga F	365.33	2216.00	808.00	228.00	49.33	101.33	18.67	29.33	16.00	97.33	29.33	24.00	52.00
M. heretunga M	.00	.00	.00	.00	.00	14.67	.00	24.00	4.00	29.33	10.67	16.00	32.00
Harpacticus sp.	.00	6.67	.00	2.67	.00	.00	.00	.00	.00	.00	.00	.00	.00
Sharknose harpacticoid	13.33	21.33	1.33	.00	.00	28.00	.00	.00	.00	.00	.00	1.33	2.67
Scutellidium sp.	.00	1.33	5.33	10.67	4.00	.00	4.00	.00	.00	.00	5.33	5.33	.00
Ostracoda	.00	1.33	.00	4.00	1.33	.00	.00	.00	.00	6.67	278.67	.00	760.00
Daphnia carinata	1.33	.00	1.33	5.33	2.67	1.33	1.33	.00	2.67	.00	.00	.00	4.00
Simocephalus vetullus	.00	.00	.00	.00	.00	1.33	.00	.00	.00	.00	1.33	.00	.00
Camptocercus sp.	2.67	.00	1.33	.00	.00	.00	.00	.00	4.00	21.33	40.00	21.33	6.67
Quinquelaophonte sp.	6.67	.00	64.00	.00	.00	17.33	1.33	8.00	6.67	17.33	32.00	4.00	17.33
Halectinosoma sp.	.00	.00	.00	.00	.00	5.33	1.33	.00	.00	1.33	2.67	.00	.00
Isopoda	.00	.00	.00	4.00	.00	.00	.00	.00	.00	.00	.00	.00	2.67
Paratya curvirostris	.00	26.67	9.33	.00	1.33	.00	2.67	.00	1.33	.00	13.33	30.67	102.67
Cryptoniscidae	197.33	49.33	.00	.00	.00	1.33	.00	.00	1.33	.00	.00	.00	1.33
Amphipoda	.00	.00	.00	.00	.00	.00	.00	.00	.00	.00	.00	.00	.00
Ctenophora	.00	1.33	.00	.00	.00	6.67	.00	.00	.00	.00	.00	.00	.00
Hydromedusae	.00	.00	.00	2.67	.00	1.33	.00	.00	.00	.00	.00	.00	.00
Anthomedusae	.00	.00	.00	.00	.00	.00	.00	.00	.00	.00	.00	.00	.00
Scyphomedusae	.00	.00	.00	.00	.00	.00	.00	.00	.00	.00	.00	.00	.00
Radiolaria	.00	5.33	.00	1.33	.00	293.33	.00	10.67	.00	.00	.00	.00	.00
Ascidacea	.00	.00	.00	.00	.00	4.00	.00	.00	.00	.00	.00	.00	.00
Fish larvae	5.33	1.33	1.33	.00	.00	8.00	.00	.00	1.33	1.33	1.33	2.67	5.33
Fish Eggs	1028.00	61.33	16.00	88.00	30.67	10.67	.00	86.67	4.00	4.00	.00	4.00	.00

APPENDIX D: Diel survey, species abundances per litre.

SPECIES\TIME PERIOD	9.93	12.83	16.17	19.33	22.42	13.00	16.00	8.75	10.50	12.17	15.75
Barnacle nauplii	993.40	162.60	30.00	497.40	82.80	.00	91.20	266.60	45.40	57.20	23.60
Copepod nauplii	301.40	24.00	25.00	20.00	22.80	25.00	25.00	44.00	12.00	25.00	155.00
Barnacle Cyprids	1.40	.00	.00	20.00	69.00	85.00	155.00	140.00	6.60	.00	.00
Brachyuran Zoae	2.60	55.40	78.00	20.00	28.40	31.40	39.00	26.60	52.00	20.00	.00
Tornaria	101.40	75.80	40.00	284.00	36.40	71.60	193.40	93.40	5.40	70.00	2.60
Gastropod Veligers	153.40	81.40	53.40	252.00	46.20	105.00	237.80	129.40	42.60	118.60	97.40
Bivalve Veligers	102.60	46.60	35.00	212.00	114.60	70.00	79.00	90.00	9.40	25.00	41.00
Mysidacea	.00	.00	.00	.00	20.00	4.00	.00	20.00	1.40	.00	.00
Acartia sp.	5.40	133.40	20.00	174.60	32.80	42.60	160.40	68.60	1.40	25.00	100.40
Paracalanus indicus	50.60	40.00	.00	35.00	34.20	62.60	6.60	38.40	.00	.00	5.60
Oithona sp.	14.60	20.00	.00	80.00	20.00	.00	4.00	32.00	.00	20.00	.00
Microcyclops sp.	5.40	20.00	26.60	26.60	.00	5.00	20.00	26.60	10.60	20.00	20.00
Temora sp.	16.00	.00	.00	20.00	20.00	.00	4.00	20.00	1.40	.00	2.00
Centropages aucklandicus	1.40	26.60	.00	20.00	30.00	20.00	1.40	.00	.00	.00	4.00
Euterpina acutifrons	45.40	140.00	.00	197.40	157.40	.00	49.00	137.40	2.60	20.00	160.40
M. heretunga	9.40	26.60	20.00	34.60	20.00	.00	32.00	24.00	1.40	32.00	20.00
Ostracoda	.00	54.20	87.20	45.80	.00	50.40	90.40	30.00	81.40	33.40	46.60
Daphnia carinata	1.40	.00	45.00	20.00	.00	.00	39.60	20.00	12.00	.00	.00
Camptocercus sp.	.00	.00	26.60	20.00	20.00	26.60	49.40	20.00	10.60	.00	.00
Paratya curvirostris	50.60	50.00	62.60	81.40	73.40	79.40	119.40	118.60	33.40	90.00	64.20
Fish Eggs	62.60	57.20	60.00	42.00	2082.80	1173.40	401.40	80.00	40.00	58.40	30.60